THE BROAD-SCLEROPHYLL VEGETATION OF CALIFORNIA

AN ECOLOGICAL STUDY OF THE CHAPARRAL AND ITS RELATED COMMUNITIES

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By William S. Cooper.

INTRODUCTION.

The characteristic vegetation of California west of the high Sierra Nevada and the Colorado and Mojave Deserts is of the type aptly described by the term "broad-sclerophyll." The use of the prefix "broad," which expresses a very general group character, in distinction to the needle-leaf of the "narrow-sclerophyll" conifers, is not without its disadvantages, since the most important chaparral species, *Adenostoma fasciculatum*, possesses a needle-like leaf. This single though important exception seems not to be sufficient cause for discarding the very expressive appellation.

Broad-sclerophyll vegetation is not confined to California, but recurs upon other portions of the earth's surface, notably the shores of the Mediterranean. The leaf character is the conspicuous and diagnostic feature, that organ being thick, stiff, and hard, ordinarily flat, and evergreen. Schimper (80) has shown that this vegetation type is everywhere correlated with a definite type of climate, namely, one with a long, dry summer and a rainy winter. Some of the broad-sclerophylls are trees, but most are scrubs. We therefore find broad-sclerophyll forest and broad-sclerophyll scrub, the latter being the more widespread and important. The present work is an ecological study of the broad-sclerophylls of California; of their relations to climate and soil and to each other. Being somewhat of a pioneer work, many phases of the problem are touched, and many lines of investigation have been opened up which could not be followed to the end. The field is a fascinating one, and a lifetime would not suffice to exhaust its possibilities.

In the Mediterranean region broad-sclerophyll scrub is known as "macchie" and "garigue"; in California it is called "chaparral." It has already been noted that the scrub is more important than the forest, both scientifically and economically. In fact, the present research began as an investigation of the chaparral alone. Because of the close relations between them, it was a simple matter to extend the field of study to include the trees. The term "chaparral" is of Spanish origin, being derived from the word "chaparra," meaning scrub oak. It seems to have been applied by the early explorers of California to the low, shrubby, dominantly evergreen vegetation which they found to be so characteristic of the Coast Ranges and the foothills of the Sierras. Locally the term is sometimes restricted to a single species, often *Ceanothus cuneatus*. The term "chamisal" is frequently applied to a pure growth of *Adenostoma fasciculatum* or "chamise."

RELATIONS OF THE CHAPARRAL TO OTHER COMMUNITIES OF SCRUB IN NORTH AMERICA.

It will be well at this point to differentiate between the chaparral and the other scrub communities of western North America. The four great types may be characterized as follows, no attempt being made to describe them minutely or to relate them to environmental conditions.

The sagebrush type.—The characteristic species, *Artemisia tridentata*, always makes a large part and frequently grows in purity over immense stretches. This is preeminently the type of the Great Basin, though extending beyond it more or less in all directions. It is sharply differentiated from the chaparral by reason of its absolutely different leaf-type and by the fact that the two overlap very slightly in range.

The desert scrub.—This is made up of a multitude of species not at all uniform superficially in ecological character. The succulents are very important, opuntias of both the cylindrical and flat-jointed forms being especially prominent. There are also thorny shrubs, some of them with soft deciduous leaves. Others, with very small leaves, have been well named microphylls. Finally, a few species in aspect recall the chaparral, the most important of these being *Covillea tridentata.* The desert scrub ranges from Arizona to Texas and southward into Mexico. In ecological character it is sharply set off from the chaparral, except for the superficial resemblance of *Covillea* just noted. This species, although it ranges to the very border of the chaparral country, mingles with that type practically not at all. Cannon (20), moreover, states that "up to this time . . . . all attempts to grow it at the Coastal Laboratory [Carmel, Monterey County] have failed." He explains this on the basis of less efficient soil temperature, but the value of that factor is of course a direct result of climatic causes. There is thus some element in the ecological make-up of the species which unfits it for life in the chaparral region, in spite of its superficial likeness. Here is a warning against the placing of too much reliance in the working out of ecological relationships upon a single conspicuous character, or even upon structural characters in general. Vital processes rather than structure are fundamental.

The deciduous thicket type.—Most important here are scrub oaks of various species, and the type is a widespread one, occurring from the Atlantic to the Pacific and from Canada to Mexico. Great stretches of foothills in the central Rockies are densely covered by it.

This is the closest of the three to the chaparral, both floristically and ecologically. In contrast to the first two, the transition between this type and the chaparral is gradual. In the Sierras and in northern California much of the scrub, dominantly evergreen, has nevertheless a large deciduous element, and there are considerable thicket areas which are composed entirely of deciduous species.

A few of the Californian sclerophylls, too, extend far beyond the average limits of the type. *Arctostaphylos pungens* ranges eastward to southwestern Colorado, where it forms an unimportant part of the deciduous thickets. Moreover, *Quercus undulata*, an important member of the Rocky Mountain thickets, itself tends strongly toward evergreenness.

The chaparral.—The chaparral may be defined as a scrub community, dominated by many species belonging to genera unrelated taxonomically, but of a single constant ecological type, the most important features of which are the root system, extensive in proportion to the size of the plant, the dense rigid branching, and pre-eminently the leaf, which is small, thick, heavily cutinized, and evergreen. This definition might be applied with equal accuracy to the macchie of the Mediterranean regions; chaparral and macchie appear to be ecologically equivalent. The chaparral is characteristically, almost exclusively, of California west of the Sierra crest and the deserts; in other words, of the region of "Californian" climate.

Because of its ecological distinctness, the Californian broad-sclerophyll scrub is entitled to a name of its own, and the term "chaparral," by reason of almost universal usage, is the obvious choice. The desert scrub and the deciduous thicket, which have been called chaparral by various authors, can easily be provided with other names if the ones used here are not satisfactory. Finally, it should be emphasized that the chaparral finds its closest ecological relative not in any other scrub community, but in the broad-sclerophyll forest, which is a response to the same type of climate.

PREVIOUS WORK.

Practically no work of purely ecological nature dealing with the chaparral has been published up to the present time. Several foresters have written excellent accounts of the aspect and behavior of the brush, especially in its relation to the forests which are associated with it. This emphasis is natural, since the chaparral is extremely important to the forester whose field of work is in California. It is essential for him to determine whether the brush can be replaced by a more valuable crop and, if not, how it can best be made to perform its important economic function of water-shed protection. In addition, there have been taxonomic studies of certain genera, and phytogeographic researches of more or less general nature, in which the chaparral has been treated. The broad-sclerophyll forest has been almost wholly neglected, except in its taxonomic aspects. It will be convenient to arrange the following brief survey of the literature under four heads, adding a miscellaneous group for certain papers that can not be classified under the three mentioned above.

(*a*) Detailed notices of taxonomic researches are outside the province of this work. Four papers dealing with difficult genera should be mentioned: Abrams on *Uva-Ursi* [*Arctostaphylos*] (2), Trelease and Brandegee on *Ceanothus* (89, 10), and Miss Eastwood on *Garrya* (28).

(*b*) Papers by foresters may be grouped in two classes: (1) those dealing particularly with chaparral; (2) descriptions of various forest reserves in which chaparral occurs. One of the former, by Plummer (74), purports to be a rather full discussion of the subject from both the purely scientific and the economic standpoints. It is totally inadequate. All the other papers by foresters deal with conditions in more or less restricted localities. Those by Boerker (9), Foster (30), Haefner (37), and Sterling (85) treat of northern California, where the chaparral is mainly of the temporary kind. Naturally the successional relations with the forest trees and the effects of fire upon these are treated with considerable detail. Subdivision of the general type into communities and subcommunities is attempted to some extent, and also the correlation of these in a very general way with habitat factors, especially slope exposure. The work has been almost wholly observational, with no exact habitat measurements and few statistical studies of the vegetation. Miller (64), studying the chaparral of northern California as a watershed cover, gives some data bearing upon successional relations. In the works of more general scope by Barber (6), Leiberg (50–56), and Sudworth (86) there is considerable material of value relating to the extent, composition, zonation, and successional relations of the chaparral in various parts of the State. E. N. Munns has put forth three papers (66–68), in which some instrumental habitat data are presented. He has also much valuable material, as yet unpublished, to which I have had access through his kindness.

(*c*) Four papers dealing with the phytogeography of southern California must be mentioned. McKenny (60) recognizes in Orange County seven formations, two of which (the mountain and the foothill formations) are mainly chaparral of various types, which are not very clearly distinguished. Hall, in his account of the San Jacinto Mountains (38), relates the vegetation to the well-known temperature zones of Merriam, and distinguishes two altitudinal belts of chaparral, the lower dominated by *Adenostoma*, the upper by *Castanopsis* and other genera. He also summarizes the obvious ecological characteristics of the average chaparral shrub, noting reduction of leaf-surface, vertical position, thickness and leathery quality, frequency of woolly pubescence (with which I would disagree), and depth of penetration of root system. Parish (71) divides southern California into five phytogeographic areas, and in consideration of the cismontane area describes the chaparral in general terms. Abrams (1) emphasizes the facts of zonation, adhering to the Merriam arrangement, and distinguishes three altitudinal belts of chaparral: the lowest, dominated by half-shrubs such as *Ramona* and *Eriogonum* (not to be classed as chaparral in my opinion); the second, in which *Adenostoma* is most important; and the upper, in which *Arctostaphylos* and other genera are in control.

The more recent phytogeographic handbooks contain brief descriptions of Californian vegetation, with more or less accurate references to the chaparral. Drude (26) applies the term to the very different desert scrub of western Texas, southern New Mexico, and northern Mexico, and has little to offer upon the sclerophyll vegetation of California. Engler's treatment (29) is similar. Schimper (80) is the first of the European geographers to give an adequate description and interpretation of the California sclerophyll vegetation. His information is mostly obtained apparently from a paper by Purpus (76). He gives a brief but adequate description of the chaparral, its general character, leaf-type, and relation to climate, and shows its likeness to the vegetation of other regions with winter rains. Warming (90) uses the term chaparral in the same sense as Drude does, but recognizes the Californian type and its relation to similar ones in other regions in the sentence: "In California maqui is known under the name of chaparral." Harshberger's account (41) is merely a compilation from Drude, Jepson, Parish, and McKenney. Clements (22) gives a brief description of the California scrub, treating it as the third of three subdivisions of the Chaparral Formation, which he conceives very broadly: the Petran (Rocky Mountain), the Sub-climax, and the Coastal Chaparral. The first two correspond with the "deciduous thicket" of the present work.

(*d*) Among miscellaneous papers should be mentioned a local descriptive article by Purdy (75); three by Cannon—one (17) showing the dependence of the Monterey pine (*Pinus radiata*) upon prevention of soil desiccation by accompanying chaparral, and two (18, 19) in which the relation of *Quercus agrifolia* and other trees to soil-moisture is treated; one by Brandegee (12) describing the recovery of the chaparral after fires; one of similar scope by Jepson (49); and an account of the distribution of species of *Eriodictyon* by Abrams and Smiley (3). Incidental references to various phases of the ecology of the chaparral are found in the publications listed in the Bibliography as Nos. 24, 27, 33, 34, 35, 44, 45, 46, 61, 62.

SCOPE OF PRESENT PAPER.

It will be seen that investigation has progressed to a more or less satisfactory degree along the following lines: taxonomy, ranges of species, range of type, its subdivisions, relation to similar types in other regions, to climate, and to fire. The ecological character of the different species has been barely touched; the same is true of the mutual relations of vegetation and habitat, and the developmental phases of the problem have been treated only so far as fire is a factor in them. These subjects are of great scientific interest in themselves. They are also fundamental to a proper understanding of the economic relations of the species. The main emphasis in this paper is laid upon these three subjects, though new material is offered along all the other lines mentioned, except taxonomy. The plan of treatment is to pass from the general to the specific. The first two chapters deal with phytogeographic relations, the next three with local units, their development and relation to habitat, and the last treats of the ecological character of the individual plant. An annotated list, with much detail that may not interest the average reader, has been added as an appendix.

The field work was of the two usual sorts: intensive instrumental and quadrat study, and extensive exploration. The former was carried on mainly in the vicinity of Palo Alto from November 1912 to September 1915, and in the summers of 1916, 1917, and 1919. The exploration covered the whole extent of the Coast Ranges from San Diego to Eureka, and a number of representative localities in the Sierras.

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I. RANGE AND CENTER OF DISTRIBUTION.

The term "center of distribution" may be understood in two ways. It may mean, on the one hand, the region in which one or more species have originated and from which they have spread; or it may signify the region where a species or a group of species attains its greatest development. The present study is not primarily concerned with origins and migrations, and therefore the second interpretation is the one used. It is true, however, that in most cases, and probably in the one here considered, a given center is a "center of distribution" in both senses. Transeau, in an important paper (88), has expressed the concept as follows:

"In using the term 'center of distribution' it is not implied that the plants have necessarily spread from these centers, but that the complex of climatic factors most favorable to the development of this type of vegetation is here localized, and that as we depart from such centers we find conditions more and more unfavorable."

Referring to a particular center he says that "within its limits, the plants have a wider range of habitats, attain a greater size, and are more abundant than elsewhere."

Adams (5) gives a list of ten criteria for the determination of centers of distribution, which include the three stated by Transeau. Six of these are susceptible of use in the present study. They are as follows:

1. Location of greatest differentiation of a type.
2. Location of dominance or great abundance of individuals.
3. Location of synthetic or closely related forms.
4. Location of maximum size of individuals.
5. Location of least dependence upon a restricted habitat.
6. Continuity and convergence of lines of dispersal.

To these I would add another, stated as follows: Location of greatest importance of the type in the climax community. There is evidence along all of these lines in support of the conclusion about to be stated. Another criterion proposed by Adams, and which would be of great use were our data sufficient, is worth stating, as a suggestion for future study: "Continuity and directness of individual variations or modifications radiating from the center of origin along the highways of dispersal."

From the evidence about to be presented I have reached the conclusion that the center of distribution of the broad-sclerophyll vegetation type of the Pacific Coast corresponds with the region known popularly as "Southern California," west of the deserts, including Ventura and Santa Barbara Counties, and also extending an unknown distance into Lower California. The evidence can best be stated under seven heads, corresponding with the six criteria proposed by Adams and the seventh which I have added. At this point I intend only to establish the location of the center. The environmental phases of the problem will be considered later.

LOCATION OF GREATEST DIFFERENTIATION OF TYPE.

Our first problem under this head is to discover which part of the general region inhabited by the type is richest in species of that type. As a corollary to this, the relative number of endemics in the different areas may be compared. The former is easily done by plotting the ranges of all the species concerned upon a single map and indicating by density of shading the numbers of overlapping ranges. The results are shown in plate 1, the large map in detail for the State of California, the small one in more generalized form for the whole region covered. Some practical difficulty was encountered in superposing the ranges of so large a number of species. The problem was solved by cutting the ranges from thin cardboard, gluing them together in their proper positions, outlining the total extent indicated, cutting away all portions where five thicknesses of cardboard or less occurred, outlining the remainder, and repeating the process. It is scarcely necessary to state that the map must be interpreted broadly and that details must be disregarded, since in only a few cases has it been possible to draw the ranges with an approach to exactness. The species considered are in general those of lists I and II (see Appendix), the deciduous ones being excluded. A few of the broad-sclerophylls were omitted because of lack of satisfactory knowledge of their ranges. The total number of species considered is 71.

From the small map we see that, broadly speaking, the type has its stronghold in California and Lower California. A few species extend northward beyond the State line; about 21 into Oregon, many of them a short distance only; 11 into Washington, and 8 into British Columbia. None occurs north of California which does not enter that State, unless we admit Howell's species of *Arctostaphylos* to consideration. The complete list of those ranging northward beyond California is as follows[1]:

Myrica californica.**
Castanopsis chrysophylla.*
  sempervirens.
Quercus chrysolepis.
  sadleriana.
Pasania densiflora.
Umbellularia californica.
Ceanothus cuneatus.
  sanguineus.**
  thyrsiflorus.*
  velutinus.**
Garrya elliptica.
  fremontii.
Rhododendron californicum.**
Arbutus menziesii.**
Arctostaphylos manzanita.
  nevadensis.*
  patula.
  tomentosa.**
Gaultheria shallon.**
Vaccinium ovatum.**

Six species extend discontinuously eastward beyond the boundaries of California:

Cercocarpus ledifolius.
Rhamnus californica.
  crocea.
Ceanothus velutinus.
Arctostaphylos patula.
  pungens.

[1] Unstarred species extend into Oregon only; those with a single star (*) into Washington, and double-starred (**) species into British Columbia.

Over the great area of the Great Basin and the Rocky Mountains covered by the lightest shading, the distribution of the few broad-sclerophylls is of course not continuous. The extreme limits of the ranges are indicated, detailed mapping in these cases being impossible.

Focusing attention upon the State of California, the following facts appear: First of all, it is seen that the Coast Ranges, the lower and middle altitudes of the Sierras, and the coastal area of southern California are the regions where the broad-sclerophylls are of importance. In two places they are absent—the Great Valley and the alpine regions of the Sierras. Over much of the former occasional plants of a number of species occur, and the region might fairly be covered by the lightest shading. This problem is discussed later (p. 77).

The development of the type in the Sierras is moderate, the belt of maximum number being in the region where the ranges of foothill and forest species overlap.

The zone of deep shading in the Coast Ranges, southward through southern California into Lower California, is the outstanding feature. Northward this follows the inner ranges, but from Monterey Bay south it borders the coast. Two spots of very special abundance are seen, one extending from Marin County to the Santa Lucias, the other covering the mountains of Santa Barbara and Ventura Counties and the San Gabriel and San Bernardino Ranges. Too much reliance should not be placed upon these, since both regions have been explored and studied with comparative thoroughness. It is true, however, that certain portions of these areas have been proved to be rich in endemics, and it may well be, therefore, that the seeming abundance of species in these spots is not wholly a false appearance.

A division into regions, with lists of species confined to each, will supplement the data furnished by the map:

In the Sierra Nevada 32 species occur, but 15 of these are found also in all the other regions and only the 3 following are confined to this region alone:

Ceanothus diversifolius.	Ceanothus parvifolius.	Arctostaphylos mariposa.

In the North Coast Ranges (San Francisco Bay being the point of division), 38 species occur, and 1 is endemic, *Arctostaphylos stanfordiana*.[1]

In the South Coast Ranges 37 species occur, and the 6 following are endemic:

Ceanothus dentatus.	Arctostaphylos andersonii.	Arctostaphylos pumila.[2]
papillosus.[2]	hookeri.[2]	vestita.[2]

[1] Here, and in other lists, several species might be added if accurate knowledge concerning their validity and range could be obtained.

[2] Members of the group of endemics characteristic of the Monterey region, *A. hookeri* and *A. vestita* being strictly confined to it.

In Southern California 47 species occur, and the following 13 are confined to the region or extend into Lower California:

Quercus engelmanni.	Ceanothus crassifolius.	Ceanothus oliganthus.
Adenostoma sparsifolium.	megacarpus.	Comarostaphylis diversifolia.
Rhus integrifolia.	spinosus.	Xylococcus bicolor.
laurina.	verrucosus.	Arctostaphylos drupacea.
ovata.		

Summarizing from the map and the lists just given, we see first that California and Lower California are the home of the broad-sclerophylls. The number of species diminishes eastward very rapidly, and northward along the coast more gradually. Further, we see that the greatest number of species occur in the Coast Ranges and Southern California. By a division into four areas we discover that the Sierras are poorest both in total number of species and in endemics; that the north and south Coast Ranges are next, being about equal in total numbers, but very unequal in endemics, the north portion having one and the south six; and that southern California stands highest with respect to both categories. Our evidence therefore points to southern California as the center of distribution of the broad-sclerophylls, and confirmation of this conclusion will be found in the paragraphs following.

LOCATION OF DOMINANCE OR GREAT ABUNDANCE OF INDIVIDUALS.

It is a matter of easy observation that the chaparral fields have their greatest extent and dominance in southern California. We have only to cite as examples the mountains of Ventura County (plate 11c), the lower ridges of the San Gabriel, the San Bernardino and San Jacinto Ranges, and the Cuyamaca Mountains (plate 11A). Without doubt the same is true of northern Lower California. Traveling northward, we find in both Coast Ranges and Sierras a gradual decrease in the vegetational importance of the broad-sclerophylls. The chaparral areas are more and more restricted, and increasingly dominated by species of successional status. In the southern Coast Ranges and Sierras the change is not so notable, but it intensifies as we reach the central portion of the State. A similar decrease is seen, very naturally, as we ascend to higher altitudes in all parts of the region. In the northern portion of the State and beyond its limits, the broad-sclerophylls lose their dominance altogether and become less and less important vegetationally. Eastward the decrease is very sharp, so that beyond the western borders of the deserts and the middle forest region of the Sierras the type is almost altogether absent as a vegetational entity.

LOCATION OF SYNTHETIC OR CLOSELY RELATED FORMS.

It is impossible, in the present state of our knowledge, to obtain accurate data upon this point. However, the very confusion which is so evident in the various taxonomic treatments of certain genera is itself evidence after a fashion. The genera *Ceanothus* and *Arctostaphylos* are classic examples. In both, the number of species proposed has been very large. Many of these fall into definite groups having close relationship within themselves, and by some authors these groups are treated as single variable species. A case in point is the group-species known commonly as *Arctostaphylos tomentosa*. From this Miss Eastwood has segregated three forms, all of which grow upon Mount Tamalpais; Abrams refers all to *A. tomentosa*. Howell has described 7 from southwestern Oregon, which Abrams reduces to synonymy. In *Ceanothus* several groups of closely related forms or species might be noted (Brandegee, 10), and in *Rhamnus* and *Garrya* the structure is similar, but on a smaller scale. It is evident that variation and hybridization are rampant among certain genera of the California sclerophylls. It is impossible to locate accurately the geographical area where these processes are most active, further than to state that they are less evident in the Sierras than in the Coast Ranges and southern California.

LOCATION OF MAXIMUM SIZE OF INDIVIDUALS.

In the case of the 9 broad-sclerophyll trees decision is easy; 4 of them, *Myrica californica*, *Quercus agrifolia*, *Q. chrysolepis*, and *Q. wislizeni*, attain their largest size in the central Coast Ranges, and the last two (according to Sargent) also in the central Sierras; 4 more, *Castanopsis chrysophylla*, *Pasania densiflora*, *Umbellularia californica*, and *Arbutus menziesii*, make their best growth in northwestern California. *Quercus engelmanni* is confined to southern and Lower California. As to the chaparral shrubs, data are scanty and unsatisfactory, especially because fire so commonly brings the shoots to an untimely end. As to the most important single species, *Adenostoma fasciculatum*, the greatest average size that I have seen was in San Benito County, in the south Coast Ranges. Other species, ordinarily shrubs, attain respectable tree size in the same general region, e. g., *Heteromeles arbutifolia* and *Prunus ilicifolia* in the vicinity of Palo Alto. The very general statement may be made that the broad-sclerophylls attain their greatest size in the coastal region—the trees in the north and the shrubs in the south.

LOCATION OF LEAST DEPENDENCE UPON A RESTRICTED HABITAT.

In southern California we find the broad-sclerophylls least confined in this respect. East of San Diego the chaparral (mainly *Adenostoma fasciculatum*) covers the gently sloping mesas, and is solid on all exposures of the lower Cuyamaca Mountains (plate 11A). The same is true, where environmental conditions are undisturbed, in certain parts of the Los Angeles and San Bernardino Valleys and on the foothills surrounding them. Farther north, in Coast Ranges and Sierras, the chaparral is more and more restricted to south-facing exposures (plate 10, A, B), the opposite slopes being occupied by other plants, first by broad-sclerophyll trees, and still farther by conifers and broad-leaved deciduous species as well. The same changes are noted in ascending the higher mountains in any part of the State.

LOCATION OF GREATEST IMPORTANCE OF THE TYPE IN THE CLIMAX COMMUNITY.

This line of evidence is closely related to the last, since a plant community which covers all slopes and exposures with fair uniformity is likely to be the climax of that region. In another place (p. 72) I will show that in certain regions the climax is dominantly of the broad-sclerophyll type; that in others the broad-sclerophylls are secondary and successional, and that there are intermediate areas where the status of these plants is uncertain; and, finally, that the region where the broad-sclerophyll type, and in particular the chaparral, is most certainly climactic, is southern California.

CONTINUITY AND CONVERGENCE OF LINES OF DISPERSAL.

If we were to select an ideal center from which migrating species might most quickly and easily reach all parts of the region where broad-sclerophylls occur commonly, we would without fail fix upon the vicinity of Ventura County. From this point easy migration routes for all the species concerned, which would be mountain ranges of moderate altitude, lead in various directions, and nowhere along their courses are there barriers of any importance. From the north two routes converge, the Coast Ranges, and the Sierras by way of the Tehachapi Mountains. Southward are the various ranges of southern and Lower California. Surely it is more than coincidence that the evidence presented along other lines points to this same region and the country immediately southeast of it.

I have endeavored in this chapter to present a picture of the range of the California broad-sclerophyll vegetation-type, principally by superposition of the ranges of the individual species; and to show, through seven lines of evidence, that the center of distribution of that type is in southern California west of the deserts, from the Santa Ynez and Sierra Madre Ranges southward into northern Lower California.

II. CLIMATIC RELATIONS.

Schimper (80) has shown clearly the constant relation between sclerophyll dominance and climate. He says:

> "The mild temperate districts with winter rain and prolonged summer drought are the home of evergreen xerophilous woody plants, which, owing to the stiffness of their thick, leathery leaves, may be termed sclerophyllous woody plants. * * * Wherever original conditions have not been altered by man the sclerophyllous trees and shrubs of districts with a moist winter always form dense and continuous woodland, which in most cases consists principally or exclusively of shrubs, but which occasionally becomes true forest, although of low or middle height only."

As to the advantage of the evergreen habit, he states that the vegetation is subject to short but frequent irregular periods of rest, sometimes due to cold, sometimes to drought; that short periods only afford simultaneously optimum conditions in temperature and moisture; the absolute optima for these two factors being entirely separate in time. It is therefore decidedly advantageous for the plants to be prepared to do their assimilative and vegetative work at all times. The regions which possess such a climate and support such a vegetation are, according to Schimper, the Mediterranean shores, the southwest extremity of Africa, southwestern and much of southern Australia, central Chile, and California. More detailed and localized works (4, 7, 8, 25, 78, 91) confirm Schimper's conclusions.

After such a thoroughly adequate, even though brief, treatment by the pioneer author, it is necessary here merely to particularize somewhat concerning the region under discussion.

The map (plate 2) is in part adapted from Reed and Kincer (77). The iso-lines indicate the percentage of total precipitation occurring in the half year April 1 to September 30. By comparing it with the map (plate 1) a remarkable correspondence will be at once evident between the region where the summer precipitation is less than 20 per cent and the region where broad-sclerophyll species are numerous. Moreover, the area of less than 10 per cent summer precipitation corresponds closely with the center of distribution of the sclerophylls, as described in the section devoted to that topic. Seasonal distribution alone, however, is not sufficient to explain the region of dominance of the broad-sclerophylls; total precipitation is only slightly less important. If the total is very high, or if atmospheric conditions are such as materially to reduce evaporation during the dry season, it may be possible for species that are less xerophytic to control; if the total is very low, true desert species will replace the broad-sclerophylls. I have therefore plotted, in a generalized way, the total precipitation in the area with less than 20 per cent summer rainfall. The iso-lines selected are of course arbitrary, but they nevertheless mark out in a striking way the areas dominated by the three great vegetation types. Where the total precipitation is more than 30 inches, the vegetation is conifer forest of some type.

The particular reasons for its presence differ in different places. In the Sierras and the isolated mountain areas of southern California the dominating cause is high total precipitation, which furnishes a sufficient amount of soil-moisture to tide the relatively mesophytic vegetation over the unfavorable season. In the higher mountains the slowly melting snows are of very great importance. In the northern end of the State, in addition to a high total precipitation, there is a decrease in the duration of the dry period. Along the northwestern coast there is, in addition to the other factors, the abundance of summer fog, which is the particular reason for the redwood forest.

The area with 10 to 30 inches of rainfall is the region of broad-sclerophyll dominance. The correspondence with the region determined upon through other lines of evidence is quite striking, even the Sacramento Valley being included (see p. 81). Only the narrow strip along the east slope of the Sierras, dominated by the vegetation of the Great Basin, must be left out. In the north Coast Ranges the broad-sclerophylls, both trees and chaparral, are of great importance, as plate 1 indicates. Observation shows, however, that the conifers are competing with them on at least equal terms (see p. 73). The climatic map, indicating conifer forest conditions for this region, is therefore not deceptive.

Finally, those regions with less than 10 inches of rainfall correspond accurately with the deserts—the western portions of the Colorado and Mojave Deserts and the Owens Valley region—and in addition the southern part of the San Joaquin Valley, which closely approaches desert conditions.

The same points are brought out in another way by table 1. The three great regions are seen by the summary to be thoroughly distinct in total precipitation, the proportion being approximately: desert 1; broad-sclerophyll 6; conifer forest 15.

The seasonal distribution in conifer forest and broad-sclerophyll regions is much alike, the summer precipitation averaging well below 20 per cent. In the desert the percentage is distinctly higher, because a number of stations east of the 20 per cent line were included in order to give a true picture of the California desert region as a whole.

Certain temperature figures are added, though the data are incomplete and their interpretation unsatisfactory. The mean annual temperature is of little use; the seasonal extremes, i. e., the means of the hottest and coldest months (in nearly every case July and January) and the mean maxima and minima of the same months are more significant. The mean annual temperature of the broad-sclerophyll region is only slightly below that of the desert. The mean of the hottest month, on the contrary, is much lower, being only slightly greater than that of the conifer forest. The striking and significant fact is that the seasonal range of temperature is far less in the broad-sclerophyll region than in either conifer forest or desert, the minima especially being decidedly above the others. This fact fits well with Schimper's elucidation of the evergreen habit as a means of utilizing short periods of favorable conditions for activity at all times of the year. The relatively narrow seasonal

TABLE 1.—*Climate and vegetation.*

Region.	Precipitation.			Temperature (° C. ; No. of stations varies).				
	No. of stations.	Total (inches).	P. ct. May 1 to Oct. 31.[1]	Mean annual.	Mean of hottest month.	Mean of coldest month.	Mean maximum (hottest month).	Mean minimum (coldest month).
Conifer forest:								
Redwood region	7	65.83	14	11.3	15.5	7.8	....	...
North Sierras	22	60.50	14.4	11.1	20.7	3.3	....	...
South Sierras	5	42.20	13.1	....	....	...	....	...
Transitional: North Coast Ranges	10	38.08	12.4	14	20.8	7.8	....	...
Broad-sclerophyll:								
South Sierra foothills	7	29.33	12	16.6	26.9	8.2	33.1	3.3
South Coast Ranges	27	20.32	11.2	14.2	19.7	8.6	27.8	2.7
Cuyamaca Mountains	10	19.92	13.3	13.7	21.4	8.3	30.7	1.6
Grassland and coastal sage-brush:								
Sacramento Valley	23	21.85	13.9	16.9	26.8	7.9	....	...
Los Angeles-San Bernardino Valley	15	16.48	11	16.8	29.1	10.5	33.7	3.9
San Joaquin Valley	31	11.21	13.4	16.9	26.8	7.9	36.9	1.7
Desert:								
Owens Valley	4	4.89	23.9	14.9	26.1	4.6	33.8	−4.0
Mojave Desert	4	3.97	28.2	17.6	29.8	7.4	40.8	1.6
Colorado Desert	7	3.11	28.9	....	....	...	....	...
Summary:								
Conifer forest	34	58.91	14.2	11.2	19.8	4.2	....	...
Broad-sclerophyll	44	21.67	11.6	14.4	20.9	8.5	28.8	2.5
Desert	15	3.82	27	15.8	27.9	5.5	36.4	−1.8

[1] The figures given here were worked out before the publication of the map (77). The difference in date of beginning and ending of summer season does not appreciably affect the results.

temperature range is of course due to the coastal location of the great mass of the broad-sclerophyll region, and it is of interest that all the other regions dominated by this type of vegetation are coastal too.

Summarizing briefly, we find that the broad-sclerophylls occur abundantly in that part of western North America where the summer precipitation is less than 20 per cent of the total, but that they dominate only that portion of this area where the total precipitation lies between 10 and 30 inches, and that the region of their dominance is also characterized by very moderate temperature extremes.

III. THE COMMUNITIES.

The terminology of plant communities is just now in a state of flux, and therefore it is too much to hope that the system employed in this paper will be satisfactory to every reader. The best that the author can do is to define his terms accurately and relate them clearly to the uses of other writers. It is therefore necessary to submit the following definitions:

The Formation. The fundamental unit of vegetation: a community relatively homogeneous ecologically in the character of its dominants, floristically in that its locally varying subdivisions are bound together by the common dominance of one or more species or by the equivalence of species ecologically near of kin, and developmentally in that within a given climatic region it has a constant successional rôle.

The Association. A vegetation unit of lower rank than the formation and contained within it; differing from other associations within the same formation with respect to any or all of the bases of the formation (ecological character, floristics, development), in minor degree, but sufficiently to cause it to stand out as a distinct entity.

These two units are analogous, respectively, to the taxonomic units, species, and variety, and one may conveniently refer to the range of a formation or association exactly as one speaks of that of a species or variety. In naming the formations I would use descriptive titles based upon ecological character, and for the associations I would employ, when possible, the names of dominants.

The Consociation, an association with a single dominant, is frequently a useful term. The word "community" is an indispensable addition to the list, being used to designate any vegetation unit without specifying its rank.

These terms must now be related to two recent systems, that of Clements (21) and that of Nichols (69). Clements applies the term *formation* to the climax community only; I would extend it to successional communities as well. Clements distinguishes between the climax units *association* and *consociation* and the successional *associes* and *consocies;* my use of *association* and *consociation* includes both types of communities. The *formation* of the present paper agrees in substance with the *association-type* of Nichols; in the use of the terms *association* and *consociation* we are in essential agreement.

THE BROAD-SCLEROPHYLL COMMUNITIES.

There are two Californian formations in which the broad-sclerophylls are the dominating element—the broad-sclerophyll forest formation and the chaparral formation. Each is in part climax, in part successional. Further, there is a broad-sclerophyll element of minor importance in the redwood forest, making a rather large part of its undergrowth. The grounds upon which the formations have been distinguished, and their range, composition, and structure, will be given here. Discussion of their relations to climate and to other communities is included in other chapters.

The broad-sclerophyll forest formation is dominated by trees, mainly sclerophyllous evergreens, but including a number of deciduous species (30.8 per cent). It is typically climax, but in this phase its extent is limited. It is successional where its range overlaps the ranges of the conifer formations, and postclimax in its overlap with the climax chaparral.

The chaparral formation is made up of shrubs, the great majority being sclerophyllous evergreens. Its climax and successional phases are both of great importance. The latter is related developmentally to the conifer climaxes and is almost totally distinct floristically from the climax phase.

THE BROAD-SCLEROPHYLL FOREST FORMATION.

This formation ranges from southern Oregon southward through the coast mountains and Sierra foothills into Lower California, reaching its limit probably in the region of Mount San Pedro Martir. Nowhere, so far as I am aware, does it dominate the country as a conifer forest, for instance, commonly does. It occurs rather in discontinuous patches, which may, however, be of considerable extent. These alternate in the main with patches of chaparral of the type which I have designated as climax. Northward the forest is the more important of the two, especially in the Coast Ranges, while southward the chaparral becomes more and more preponderant. In the north there is overlap also with the ranges of the *Sequoia sempervirens* and the *Pseudotsuga* associations of the Pacific conifer formation, and in the Sierras with the formations of the conifer forest region.

The number of dominant species is not large. In the following list a single asterisk indicates importance also in the conifer forest chaparral; and two asterisks, in both that and the climax chaparral.

Sclerophylls.

Myrica californica.
Castanopsis chrysophylla.*
Quercus agrifolia.
Quercus chrysolepis.
engelmanni.
wislizeni.**
Pasania densiflora.*
Umbellularia californica.
Arbutus menziesii.

Deciduous.

Quercus kelloggii.*
lobata
Acer macrophyllum
Aesculus californica

Several associations occur, easily recognized because of their relative constancy and wide distribution. Many individual localities would fit into none of them, and therefore in a minute study numerous transitional units might be described.

Pasania-Quercus-Arbutus Association.—This community is characteristic of the lower altitudes of the North Coast Ranges, a region very complex and rather difficult to understand vegetationally, since two or more types which are climactic nearby meet here and overlap, finding conditions that are reasonably favorable to all. The redwoods thoroughly dominate the coast. East of them *Pseudotsuga mucronata* is the commanding species, but shares its rule with the broad-sclerophyll association about to be described. Chaparral and grassland communities also occur, but these are plainly successional. The *Pasania-Quercus-Arbutus* association is itself somewhat of a transitional unit between broad-sclerophyll and conifer types, for it rarely occurs without at least a sprinkling of conifers, especially *Pseudotsuga*, and its principal species occur commonly as an understory of the *Pseudotsuga* and *Sequoia* forests.

The most important species of the formation are *Pasania densiflora*, *Quercus chrysolepis*, and *Arbutus menziesii*, and these attain great size. Other tree species occurring more or less commonly are *Quercus kelloggii*, *Castanopsis chrysophylla*, *Umbellularia californica*, *Acer macrophyllum*, *Æsculus californica*, and *Cornus nuttallii*. The association ordinarily possesses two layer societies—one of shrubs, including *Corylus rostrata californica*, *Vaccinium ovatum*, and *Gaultheria shallon*, and one of herbs and ground-shrubs, a mixture of typically oak-forest species and those commonly associated with the redwood and douglas fir.

The transitional phases of the association will be made evident by description of two areas, one in the interior of the Coast Ranges, where *Pseudotsuga* is the competing tree, the other on the edge of the coastal redwood region.

The first locality is in Trinity County, on the north-facing slope of the Mad-Trinity Divide. The dominant tree, *Pseudotsuga*, grows here magnificently, many specimens attaining a diameter of 2 meters. *Abies concolor* and *Pinus lambertiana* also occur. Beneath the conifers there is an understory of broadleaf trees, nearly all sclerophylls. *Castanopsis chrysophylla* is the most abundant, and *Pasania*, *Arbutus*, and *Acer macrophyllum* also occur. This assemblage might here be termed a layer society. *Corylus rostrata californica*, *Cornus nuttallii*, and *Ceanothus integerrimus* form a second stratum, and a third is composed of herbs and ground shrubs: *Vancouveria* sp., *Polystichum munitum*, *Berberis* sp., *Gaultheria shallon*.

The other is the valley of the South Fork of the Eel River, in Humboldt County. In the vicinity of Garbersville and for several kilometers north of it (downstream), the north slopes and ravines are forested with *Pasania densiflora*, *Quercus kelloggii*, *Q. chrysolepis*, *Q. garryana*, *Arbutus menziesii*, *Umbellularia californica*, *Æsculus* *californica*, *Acer macrophyllum*, and *Pseudotsuga*, making a rather typical specimen of the *Pasania-Quercus-Arbutus* association. The first redwoods appear in groups of large trees on the valley bottom, with scattered individuals on north slopes (plate 8A). This continues for 15 kilometers or more, then for several kilometers there is an almost pure forest of *Sequoia* on north slopes with the *Pasania-Quercus-Arbutus* association on south exposures. Finally the forest becomes nearly pure *Sequoia* on all slopes, the broad-sclerophylls gradually disappearing as a distinct community, though remaining to some extent as a layer society, particularly *Arbutus* and *Pasania*.

Quercus agrifolia-Arbutus Association.—This unit is coastal, occurring from the northern limit of *Quercus agrifolia* in Mendocino County to the southern limit of *Arbutus* in Los Angeles County. It is thus characteristic of the outer central Coast Ranges, where it is the dominant cover on north-facing slopes. It is particularly well developed in the San Francisco Bay region and southward to the Santa Lucia Mountains. The character tree is *Quercus agrifolia*.[1] *Arbutus menziesii* is next in importance, but varies greatly in abundance in different localities. *Æsculus californica*, a deciduous species, is usually prominent, and *Umbellularia californica* is equally so. *Acer macrophyllum* is frequently important in the more mesophytic localities. In areas that are transitional with the *Sequoia* association, *Pasania*, *Quercus chrysolepis*, *Q. kelloggii*, and *Sequoia* itself occur. Since a typical area of this association is described in another part of this paper (p. 38), it will be unnecessary to go further into details here. Station 7 at Jasper Ridge is representative in every respect (plates 14A, 8B).

Quercus agrifolia Consociation.—South of the southern limit of *Arbutus* (Los Angeles County) the community is continued as a consociation dominated by *Quercus agrifolia*. This is rather prominent in the lower altitudes of the west slope of the Cuyamaca Mountains.

Umbellularia Consociation.—*Umbellularia* occurs scattered through the *Quercus agrifolia-Arbutus* association, and in others as well, but it also forms pure growths, especially in the central Coast Ranges, occupying moist ravines and canyon bottoms. These groups of *Umbellularia* stand out strikingly above the other trees, being conspicuous by reason of their light green color and conifer-like form. The shade is very dense and undergrowth almost lacking. *Umbellularia* itself, however, is able to germinate successfully under such conditions.

Quercus agrifolia-lobata Association (plate 9A).—This is characteristic of the broad valleys and gentle footslopes of the central

[1] In some places, especially in the inner Coast Ranges, it is replaced by *Q. wislizeni*, and thus another association might be distinguished.

Coast Ranges, being locally of considerable importance in the San Francisco Bay region. The dominant species are *Quercus agrifolia* and *Q. lobata*, the latter being deciduous. The trees as a rule stand far apart, producing a park-like landscape, and it is in such places that the largest specimens of both species occur. One tree of *Q. agrifolia* near Palo Alto is 2.1 meters in diameter breast-high. A specimen of *Q. lobata* west of Clear Lake is of the same diameter, with a spread of branches of 47 meters. Much larger trees of the latter have been reported. Other species are of occasional occurrence. In the Palo Alto region large specimens of *Umbellularia*, *Arbutus* and *Prunus ilicifolia* make a small part of this association. Because of the wide scattering of the trees, the ground between is in most places under cultivation. Near Palo Alto, however, there are a few localities which retain their original vegetation, because they have long been included in certain large estates. In such areas one finds the two oaks of all sizes from seedlings to large mature trees. Most of the young ones occur in indefinite groups in the opener places, while the mature specimens completely dominate the ground beneath them. Three layer societies occur. The first, of tall shrubs, includes *Rhamnus californica*, *Heteromeles arbutifolia*, *Sambucus glauca*, and *Rhus diversiloba*. The low-shrub society includes *Rubus vitifolius*, *Symphoricarpos racemosus*, and *Solanum umbelliferum*. *Micromeria chamissonis* is dominant in the ground layer society. Further details concerning this very interesting association will be given in a future paper upon the communities and successions of the Palo Alto region.

Quercus chrysolepis-kelloggii Association.—The associations so far described are distinctly of low altitudes. The present one belongs to the higher Coast Ranges and southern California mountains and to the middle altitudes of the Sierras. It is preeminently a north-slope forest, but localities are common enough where it occurs on other exposures as well, seeming like a true climax. The most important tree species is the broad-sclerophyll *Quercus chrysolepis; Q. kelloggii*, deciduous, is often a close second. Others are *Arbutus*, *Umbellularia*, *Acer macrophyllum*, *Pasania*, *Æsculus*. Since the association has so great a range, the subordinate vegetation varies greatly. It shows broad transition areas with neighboring associations. Its close relation to the *Pasania-Quercus-Arbutus* association is at once evident, and it is not strange, therefore, to find areas that can not be placed with certainty in either. Again, just as the *Pasania-Quercus-Arbutus* association passes into the *Sequoia* forest as an understory, so also does the *Quercus chrysolepis-kelloggii* association into the pine forests of the high Coast Ranges and the Sierras. In fact, in the Sierras it is commoner to find the community as an understory beneath *Pinus ponderosa* and *P. lambertiana* than as a dominating type. In the mountains of southern California the group forms a similar understory beneath *Pseudotsuga macrocarpa.* Upon the xerophytic side there is transition to the chaparral. Such areas have so individual a stamp that I have been accustomed to refer to them as "dwarf forest." An excellent example is found upon the north slope of Mount Tamalpais (Marin County), near the summit. *Quercus chrysolepis* and *Q. wislizeni*, growing in dense thickets 3 to 5 meters in height, are dominant, an occasional full-sized tree of *Q. chrysolepis* rising above the general level. With them grow other species: *Quercus agrifolia, Pasania, Arbutus, Umbellularia, Torreya californica,* and the chaparral shrubs *Arctostaphylos tomentosa* [*A. glandulosa* Eastwood], *Ceanothus sorediatus,* and *Castanopsis chrysophylla minor.*

Quercus chrysolepis Consociation (plate 9B).—In the middle altitudes of the Sierras, dominated by the pines and *Pseudotsuga, Quercus chrysolepis* growing almost pure has a distinct successional rôle. Upon the great talus accumulations at the bases of the Yosemite cliffs certain chaparral shrubs are the pioneers. These are followed by a dense, pure growth of *Quercus chrysolepis* which seems to persist for a long time, as the live-oak forest is the most conspicuous feature of such areas. The talus piles that are manifestly oldest, with much accumulation of humus, support a mixture of the oak and *Pseudo suga.*

A few concluding remarks in summary will gather together the main points in the discussion of the broad-sclerophyll forest formation. It is plain that the group as a whole is the fundamental unit, the minor divisions being closely tied together by a number of binding species. The transition zones between associations of the formation and with other formations are broad, so that accurate delimitation is difficult. The broad-sclerophyll communities, wherever they adjoin the conifer forest communities, pass into them as layer societies. There is a very close habitat relation between the broad-sclerophyll forest and the climax chaparral, in that in the main they overspread the same range, occupying areas of comparatively slight physical differences. The question of climax, therefore, whether one or the other or both, is difficult. My conclusions will be given in a later section.

THE CHAPARRAL FORMATION.

It was pointed out at the beginning of this chapter that the chaparral formation, homogeneous in the ecological character of its dominants, at least so far as anatomical structure is concerned, embraces two associations which are very distinct floristically and developmentally. Separate treatment of these will be the best method of presentation.

The Climax Chaparral Association.

The climax chaparral is the dominant community over the whole of the southern Coast Ranges and the mountains of southern California and northern Lower California. Only the highest summits, controlled by conifers, and the more mesophytic north slopes, inhabited by broad-sclerophyll forest, must be excepted. Northward in the north Coast Ranges the chaparral shares its control more and more with the broad-sclerophyll trees, and opposite the northern end of the Sacramento Valley it disappears entirely as a dominating community. In the southern Sierras it is of great importance, occupying a wide belt in the foothills. In the northern Sierras its continuity is broken, and this is not strange, since the conifers of the montane forest here reach the valley floor. The present range of the climax chaparral is indicated in a very general way by the range of its most important species, *Adenostoma fasciculatum* (plate 3). In addition, I believe that there are certain extensive areas now inhabited by grasses and by half-shrubs that climatically and potentially are chaparral regions (p. 76).

Since the climax chaparral is by far the most widely extended and diversified of the broad-sclerophyll communities, it is natural that the present list of species should be the longest. The following are all evergreen, except that *Quercus dumosa* is barely so. One asterisk (*) indicates that the species is also of importance in the conifer forest chaparral; two asterisks (*) that it is important in that and also in the broad-sclerophyll forest.

Castanopsis chrysophylla minor.*
Quercus chrysolepis.**
  dumosa.
  durata.
  wislizeni frutescens.**
Dendromecon rigidum.
Heteromeles arbutifolia.
Cercocarpus betulæfolius.
Adenostoma fasciculatum.
  sparsifolium.
Prunus ilicifolia.
Xylothermia montana.
Cneoridium dumosum.
Rhus integrifolia.
Rhus laurina.
  ovata.
Rhamnus californica.*
  crocea.
Ceanothus crassifolius.
  cuneatus.
  dentatus.
  divaricatus.
  hirsutus.
  megacarpus.
  papillosus.
  rigidus.
  sorediatus.
  verrucosus.
Garrya elliptica.
Comarostaphylis diversifolia.
Xylococcus bicolor.
Arctostaphylos andersonii.
  glauca.
  hookeri.
  manzanita.
  montana.
  pumila.
  stanfordiana.
  tomentosa.
  vestita.
Eriodictyon californicum.

With so large a list of species there is naturally great diversity in the composition of the association. Anyone given to splitting of hairs would easily separate many communities of lower rank. This is in part due to slight habitat differences, but also in an important degree to the great number of species with restricted range and to the frequent occurrence of fires, which result in multitudinous combinations of species, depending upon which are able to survive or to repopulate the area burned. It is easy to recognize, however, throughout the length and breadth of the region, one striking and characteristic consociation, for *Adenostoma fasciculatum* covers many hundreds of square miles in practically pure dominance. The range of the *Adenostoma* consociation is indicated on the map (plate 3). Other species, too, completely control certain areas, but it is far commoner for these to mingle with each other and with *Adenostoma* in an endless number of combinations and proportions. In 87 listed localities in all parts of the State, the following occurrences of important and widespread species are noted:

Adenostoma fasciculatum	75	Cercocarpus betulæfolius	19
Arctostaphylos (all species)	50	Quercus wislizeni frutescens	11
Heteromeles arbutifolia	26	Rhamnus californica	10
Ceanothus cuneatus	25	Quercus chrysolepis	10
Quercus dumosa and Q. durata	23		

Such being the condition, it avails little to attempt to distinguish minor units within the association. It is more reasonable to express the differences by noting the dominance of one or more species in particular cases. One fact, however, must be brought forward. The genus *Arctostaphylos* gives its stamp to certain localities in a very characteristic way. No one species is dominant throughout. *Arctostaphylos tomentosa* is by far the most important, ranging over the whole region. *A. glauca* is abundant in the southern half of the State and *A. manzanita* in the northern, and several others are prominent locally. This phase nearly everywhere accompanies the *Adenostoma* consociation, occupying the less xerophytic north-facing slopes where these are not sufficiently moist to permit the forest to exist, and at higher altitudes replacing the *Adenostoma* consociation on the south slopes, the north exposures being forested. The combination is well shown at Jasper Ridge, described in the next chapter.

The Conifer Forest Chaparral Association.

The range of this community is nearly coextensive with that of the montane conifer forest, spreading to some extent into the region of the subalpine conifer forest. Its home is, therefore, in the middle altitudes of the Sierras, with extensive colonies throughout the higher mountains of northern California and Oregon, the north Coast Ranges, and the mountains of southern California. It reaches its best development where the forest which controls it is best developed, and therefore its true center is in the northern Sierras. Accurate altitudinal data are unavailable, and the patchy distribution makes close determination impossible, but the lower limit may be placed roughly at the lower limit of *Pinus ponderosa*, which is very near to the valley-level at the northern end of the Sierras and rises gradually southward. Naturally there is extensive overlap with the range of the climax chaparral which dominates the foothill region in imperfect manner. The upper limit is equally indefinite.

Above the ranges of the dominant trees of the Montane Forest the chaparral species become gradually fewer. At least one (*Arctostaphylos nevadensis*) reaches timberline in the Yosemite region (39).

The following list includes those species which are of importance in the conifer forest chaparral in various parts of its range. Many others, of course, occur occasionally, especially where the range of the formation overlaps that of another. Species marked with a single asterisk (*) are of importance also in the broad-sclerophyll forest, those with two asterisks (**) in the climax chaparral, and those with three in both.

Sclerophylls.

Castanopsis chrysophylla minor.*	Pasania densiflora echinoides.*	Arctostaphylos mariposa.
sempervirens.	Rhamnus californica.**[1]	nevadensis.
Quercus chrysolepis.***	Ceanothus cordulatus.	patula.
sadleriana.	velutinus.	pungens.
vaccinifolia.	Garrya fremontii.	viscida.
wislizeni.***	Arctostaphylos drupacea.	

Deciduous.

Corylus rostrata californica.	Amelanchier alnifolia.	Cercis occidentalis.
Quercus breweri.	Prunus demissa.	Acer glabrum.
garryana.	emarginata.	Ceanothus integerrimus.
kelloggii.*	subcordata.	sanguineus.

The conifer forest chaparral association is at least as variable as the climax chaparral. This is due in part to great variation in habitat and also in an important degree to what may be termed accidental causes, for since the community owes its existence in large part to the frequent destruction of the forest by fire, the population of a given area must depend largely upon what species are producing seed in its immediate vicinity. The association has been carefully studied by the U. S. Forest Service, since its occurrence within the belt of merchantable timber gives it great economic importance. A number of reports have been published (see introduction) and many more are still in manuscript, and to these I have had access through the kindness of the officials of District 5 in San Francisco.

Since the work of the Forest Service upon this community greatly outweighs mine, and since more of it is soon to be published, I will not attempt detailed subdivision. A few general features are worth pointing out, however. In the lower and drier portion of the yellow-pine belt of the Sierras one combination is of great importance. This is made up of *Arctostaphylos viscida* and *Ceanothus integerrimus*, the former being especially conspicuous because of its beautiful gray foliage. It is particularly widespread in the regions surrounding the old placer diggings, where the timber was cut and burned off more than half a century ago. In the upper and moister portion of the pine belt and the lower part of the Subalpine Zone the areas of chaparral show greater floristic diversity, and a great

[1] Principally in its two varieties, *R. c. tomentella* and *R. c. rubra*. The latter is deciduous.

number of consociations and mixtures might be distinguished. In the higher northern Sierras half a dozen species are of paramount importance. These are *Castanopsis sempervirens*, *Quercus vaccinifolia*, *Prunus emarginata*, *Ceanothus cordulatus*, *C. velutinus*, *Arctostaphylos nevadensis*, and *A. patula*. They occur in all possible combinations, so that a classification for one region may not fit another at all. We should also mention the thickets of deciduous oaks, especially *Quercus kelloggii* and *Q. garryana*, which are so extensive in the mountains of Trinity County and northward. These species, ordinarily trees, here grow in dense masses like the chaparral, forming a connecting link ecologically with the deciduous oak thickets of the Rocky Mountain foothills.

The following outline of the broad-sclerophyll communities will serve as summary to this chapter, all being climax except those specially noted:

A. Broad-sclerophyll forest formation.
  1. Pasania-Quercus-Arbutus association.
  2. Quercus agrifolia-Arbutus association.
    2*a*. Quercus agrifolia consociation.
    2*b*. Umbellularia consociation.
  3. Quercus agrifolia-lobata association.
  4. Quercus chrysolepis-kelloggii association.
    4*a*. Quercus chrysolepis consociation (successional).

B. Chaparral formation.
  1. Climax chaparral association.
    1*a*. Adenostoma and other consociations and various mixtures.
  2. Conifer forest chaparral association (successional).
    2*a*. Numerous vague minor units.

IV. VEGETATION AND HABITAT.

THE LOCALITY FOR INTENSIVE STUDY.

THE PALO ALTO REGION.

For intensive study of vegetation and habitat it was necessary to find a spot as nearly representative as possible, affording opportunity for comparison of related communities and favorably situated with respect to a base of operations. The vicinity of Palo Alto satisfied these requirements, the botanical laboratory of Stanford University furnishing facilities for indoor work.

Palo Alto is situated in the central Coast Range region, near the southern extremity of San Francisco Bay, from which it is but 3 km. distant. The lowland upon which it lies extends along the southwest shore and is commonly spoken of as a northwestward extension of the Santa Clara Valley. Southwestward from the town rise the Santa Cruz Mountains, the crest, ranging from 512 to 850 meters in height, being 11 km. distant. The northeast face of the range is a fault scarp, and therefore abrupt. There is, nevertheless, a zone of foothills between the main mountain front and the valley, in the vicinity of Palo Alto 5 km. broad and attaining a height of 246 meters. The altitude of Palo Alto itself is but 17 meters.

The topographic diversity just outlined, together with the influence of the ocean, which is distant from Palo Alto 25 km. over the Santa Cruz Range, produces very great climatic differences within short distances. Thus, the annual precipitation at Palo Alto is 66 cm., while on the mountain summits, only 15 km. away, it is 139 cm. (23, p. 186). At the ocean shore the precipitation is again light, 75 cm. being recorded at one station. The summer fogs, which regularly cover the mountains but rarely invade the valley, are also of profound climatic importance.

In correlation with topographic and climatic diversity we find equal diversity in the vegetation. The prevailing type in the fog-bathed mountains is the redwood forest; the well-watered mountains without fog support a vegetation made up of evergreen oaks, madroño, and Douglas fir; the foothills and drier mountain sides are clothed with chaparral except where local conditions, such as steep north slopes, permit the development of oak forest; the gentle slope from foothills to bay was originally covered by chaparral, open oak forest, and salt marsh, all of which have been more or less disturbed by cultural operations. For an account of the redwoods and their relation to rainfall and fog, the reader is referred to a former paper (23).

JASPER RIDGE.

The locality chosen for quadrat and instrumental study was one of the higher foothills, 7 km. southwest of Palo Alto, known locally as Jasper Ridge. It is a hilly mass, approximately 10 km. northwest and southeast, by half as much in the other dimension. It is nearly surrounded by the valleys of San Francisquito, Los Trancos, and Corte de Madera Creeks, the floors of which range in altitude from 60 to 120 meters. The average height of the crest of the ridge is approximately 180 meters, and the highest point, near the southeastern end, 246 meters. The mass here has a rather broad, rolling summit, but the slopes are considerably dissected by ravines. Northward and northeastward from Jasper Ridge the hills are lower, but southwestward, across the valley of Corte de Madera Creek, the main front of the Santa Cruz Mountains rises to an altitude of 600 meters.

The surface rock of the main part of the ridge is probably the Chico sandstone of Upper Cretaceous age (14). There are two areas of the Franciscan formation of considerable extent and one outcrop of serpentine, but the area studied is entirely within the limits of the presumptive Chico. This rock weathers into a uniform coarse yellow sand. In most places the layer of residual soil is very thin, but on a few level spots there is a greater depth. In excavations in such places the sand is seen to merge gradually into the undecomposed rock, which is found practically intact at a maximum depth of a meter or a little more. On steep hillsides the soil is irregular in depth, with rock outcrops alternating with sand pockets. The greatest accumulations are naturally at the foot of the steepest slopes, where the sand contains many angular fragments of considerable size. Of the ten stations studied, eight possess a uniform soil of the type just described. The other two show local differences which are of sufficient importance to affect considerably the vegetation growing on them.

At first thought it would seem absurd to devote a paragraph to the climate of so limited an area as Jasper Ridge, after the climate of the region as a whole has been discussed. In California, however, such is not the case. One can not assume that the climates of two places are alike because they are but a few kilometers apart. Witness the great difference in rainfall already noted between Palo Alto and the summit of the Santa Cruz Range. In the matter of rainfall, Jasper Ridge lies between the above stations, as it does in position. The precipitation for a number of stations in the Santa Clara Valley, foothills, and Santa Cruz Mountains in the season 1913–14 (a very wet year), was as follows (see 23, p. 185):

		cm.
Valley:	San Jose	47.83
	Palo Alto	62.15
Foothills:	Jasper Ridge	103.71
Mountains:	King's Mountain	169.25
	Ben Lomond	197.66

Assuming that the proportion between the stations will hold roughly constant for a succession of years, the normal rainfall at

Jasper Ridge, calculated from those of San Jose and Ben Lomond Weather Bureau Stations, is about 80 cm.

It seems probable that Jasper Ridge has a smaller total of fog than either the valley or the mountains. The true ocean fogs rarely reach it and the "bay" or "tule fogs," which are frequent during the forenoon in the lowland, do not ordinarily rise so high. The average midday temperature is probably higher than in the valley because of the proximity of the bay to the latter, and also higher than in the mountains because of altitude and fog. Temperature and fog affect vegetation through their influence upon the evaporating power of the air, and it is quite certain that the evaporation-rate is much higher upon Jasper Ridge than in the mountains, and almost as certain that it is higher than in the valley, because of distance from the bay, absence of fog, and probably higher mid-day temperature. We therefore conclude that Jasper Ridge is far more xerophytic in climate than the mountains and perhaps somewhat less so than the valley. It may be, however, that the greater rainfall is neutralized by the higher evaporation-rate. The evidence of the vegetation is that there is little climatic difference between the ridge and the valley.

THE VEGETATION.

The vegetation of Jasper Ridge was originally mainly chaparral. Large portions have been cleared of the bushy growth, quite certainly within a century, and the cleared areas are now expanses of wild oats (*Avena fatua* and *A. barbata*), with scattered oaks, especially *Quercus douglasii*, which is peculiarly characteristic of such secondary areas. *Quercus agrifolia* and *Q. kelloggii* are also frequent, and there is a considerable scattering of shrubs of the species that frequent such cleared areas: *Ceanothus cuneatus*, *Heteromeles arbutifolia*, *Baccharis pilularis*, and especially *Rhus diversiloba*.

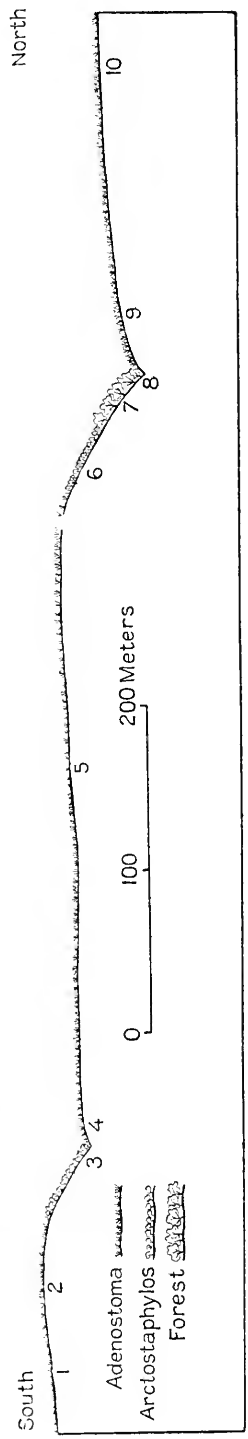


Fig. 1.—Profile of a part of Jasper Ridge, drawn approximately to scale, showing topography along trail, distribution of plant communities, and location of stations.

The original vegetation still remaining is comprised in several large patches, the two principal ones being at the northwest and southeast extremities of the ridge. It is true that these are mere remnants, but they are of sufficient size to show absolutely natural conditions, except along the edges. The studies were made in the area at the southeast extremity, which covers approximately 2.5 sq. km. and includes the highest point of the ridge. It possesses rather bold relief, including several summits and ravines, one of which is decidedly abrupt. The extreme range of altitude is from 184 meters at the bottom of the deepest ravine to 246 meters at

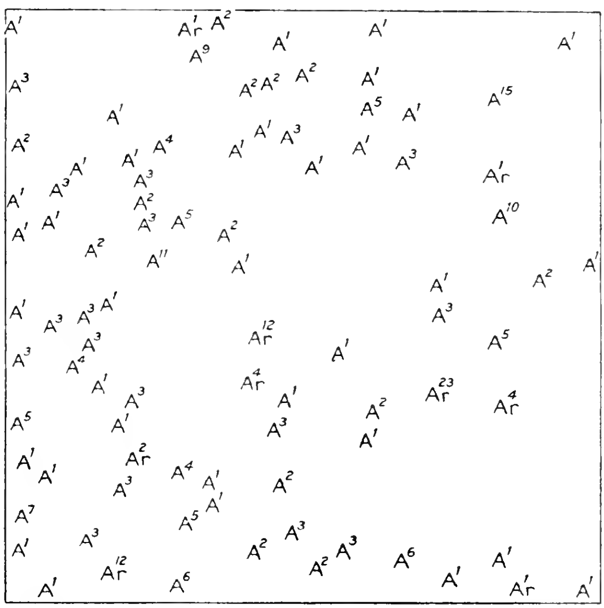


FIG. 2.—Quadrat at station 1, 5 meters square Note abundance of individuals of *Adenostoma*, which, however, are small and do not control the area. For symbols in this and succeeding quadrats see footnote, p. 34.

the highest hilltop. The vegetation of the area is mainly chaparral. The *Adenostoma* consociation covers the south-facing slopes and the summits and is by far the most extensive type; *Arctostaphylos* is dominant upon the gentler north-facing slopes; and on the north-facing slope of the deepest ravine is a typical area of the *Quercus agrifolia-Arbutus* association of the broad-sclerophyll forest. It is thus an ideal place in which to study the various communities of broad-sclerophyll vegetation and their relations to habitat and to each other.

For quadrat and instrumental study a series of ten stations was determined upon, lying on an approximately north-south line which crossed all slopes and vegetation types, giving two or more examples of each. A trail was cut through the brush connecting these with each other and with a nearby road. The distance between the extreme stations was approximately 800 meters.

Stations 7 and 8 represent the forest and the remaining eight the chaparral. Of the latter, stations 1, 4, 5, 9, upon south-facing slopes, and 2 and 10, on nearly level summits, were in areas of *Adenostoma* dominance, and stations 3 and 6, upon north-facing slopes, in *Arctostaphylos* dominance. Quadrats were charted in six of these. A number of statistical quadrats confirm the results.

Station 1.

This has the poorest vegetation of any. A quadrat 5 meters square is represented in figure 2.[1] The species within it are given below in order of abundance, with the number of plants of each and the number of individual stems. Exact statistical study of chaparral vegetation is difficult, because of the common habit of growing in clumps and the frequent impossibility of readily determining the limits of a single group. The figures given are therefore not absolutely accurate.

	Clumps.	*Stems.*
Adenostoma fasciculatum	81	219
Arctostaphylos tomentosa	9	60
Total	90	279

Heteromeles arbutifolia is occasional nearby. The bushes are all small, ranging from 3 to 12 dm. in height, most of them nearer the former figure. In spite of the large number of individual plants, the ground is poorly controlled, large areas being entirely unshaded. Herbaceous growth is practically absent, the quadrat showing not a single plant at the time when it was plotted (August 25). There is no humus superficially visible, and very scanty litter.

Station 2.

This station is on the highest point of Jasper Ridge and therefore most thoroughly exposed to atmospheric agencies. Moreover, with station 1, it differs in soil character from the other eight, as will be later shown. The vegetation is of better appearance than that of station 1, but is still low and scattered, so that it is possible to walk between the bushes in many places. No chart quadrat was

[1] The symbols used in this and the following quadrats are given here. Exponents, except in figure 6, indicate number of stems in a clump.

A.	Adenostoma fasciculatum.	B.	Baccharis pilularis.	Qa.	Quercus agrifolia.
Ab.	Arbutus menziesii.	C.	Ceanothus sorediatus.	Qd.	Quercus durata.
Ae.	Æsculus californica.	D.	Diplacus glutinosus.	Qw.	Quercus wislizeni.
Ar.	Arctostaphylos tomentosa.	H.	Heteromeles arbutifolia.	R.	Rhus diversiloba.
As.	Aster radulinus.	Ho.	Holodiscus discolor.		

made, but a statistical quadrat of 5 meters square gave the following results:

	Clumps.
Adenostoma	98
Arctostaphylos	4
Total	102

Quercus durata is rather frequent in the vicinity and *Heteromeles arbutifolia* and *Quercus wislizeni* also occur. Undergrowth is hardly more noticeable than in station 1. There is practically no humus and very scanty litter.

STATION 3.

A short distance north of station 2 a moderate slope begins, which extends downward for a distance of 75 meters to the bottom of a shallow ravine. From the summit for a little distance downward,

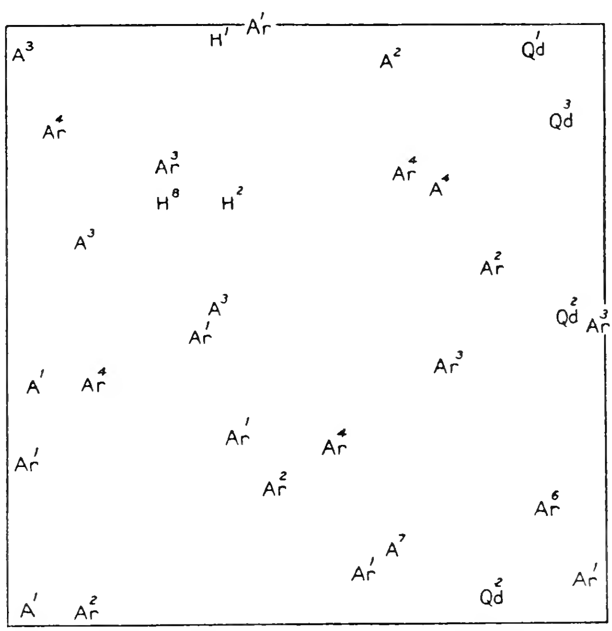


FIG. 3.—Quadrat at station 3, 5 meters square. Note fewness of individuals, mostly *Arctostaphylos*, which nevertheless thoroughly control the area.

Adenostoma is predominant, but a gradual change is noted, until the lower half is seen to be dominated by *Arctostaphylos* and *Quercus durata*, with *Adenostoma* a decided minority. The size of the shrubs also increases gradually, until near the bottom of the slope they average 2 meters in height. The density is such that the ground is entirely dominated, and the only way to travel is on one's hands and knees below the zone of tightly intertangled branches. The enormous woody masses which frequently form the bases of the *Arctostaphylos* and *Adenostoma* clumps are very prominent here, occupying a surprising amount of the ground area. The quadrat shown in figure 3 gives the following summary:

	Clumps.	*Stems.*
Adenostoma	7	23
Arctostaphylos	18	44
Quercus durata	4	8
Heteromeles	3	11
Total	32	86

An occasional plant of *Diplacus glutinosus*, a half-shrub, is found here, badly off for light. Depauperate specimens of *Symphoricarpos racemosus* are rather frequent. Herbaceous growth occurs, but not in great amount. The most abundant is *Aster radulinus*, which produces nothing but basal leaves under the solid chaparral cover. The only other is the fern *Gymnogramme triangularis*. The woody bases of the shrubs are covered with mosses and small *Cladonias*. Humus is in fair amount and litter is abundant. Where the trail crosses the ravine bottom a single young specimen of *Quercus agrifolia* suggests a tendency toward mesophytic forest conditions.

Station 4.

Crossing the ravine, the vegetation is seen to change, with no transition zone, to *Adenostoma* dominance. The striking contrast is manifestly related to the sharply angular change of slope at the ravine bottom. Station 4 is exactly opposite station 3 and at an equal height. The bushes, averaging 1.2 to 1.5 meters, are decidedly better in appearance than those of stations 1 and 2, and the ground is controlled by them to a much greater degree, though not completely. The quadrat (fig. 4) contains the following:

	Clumps.	*Stems.*
Adenostoma	24	133
Arctostaphylos	5	42
Quercus durata	3	4
Total	32	179

The undergrowth is exceedingly sparse, including a few individuals of *Aster radulinus* and *Gymnogramme triangularis*. Humus is scanty, but there is considerable litter beneath the shrubs. A plant of *Quercus wislizeni* close to the quadrat has three trunks 2.5 meters high, standing well above everything else.

Station 5.

Going northward up the gentle slope, we pass through vegetation like that of station 4, but becoming lower and less dense. There are frequent areas where one may walk between the bushes, many of which are of low stature. *Adenostoma* is everywhere dominant, and *Arctostaphylos*, *Heteromeles*, *Quercus durata*, and *Q. wislizeni* are also present. Undergrowth is practically absent, and humus and litter are scanty.

Station 6.

Passing over the second summit, we find *Adenostoma* still dominant and greatly increasing in size and controlling power. Descending the steep north slope a short distance, we encounter a gradual change to conditions like station 3. Here station 6 was established. The

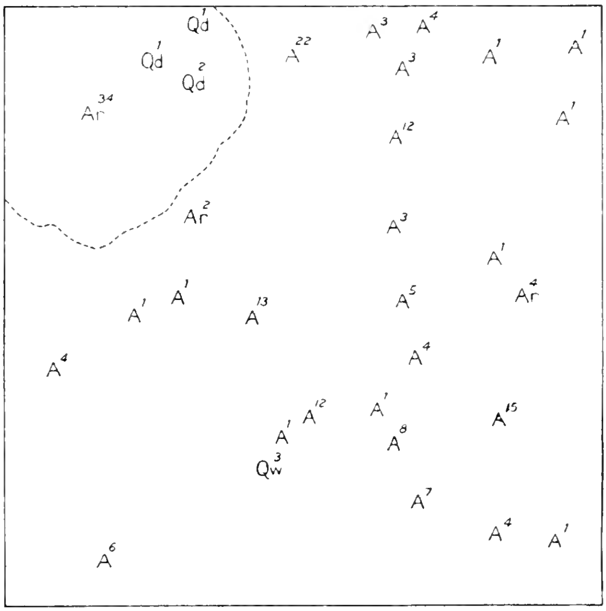


Fig. 4.—Quadrat at station 4, 5 meters square. Note relative fewness of individuals of *Adenostoma*, which control the area with fair completeness. The dotted line indicates the area dominated by the large clump of *Arctostraphylos* (Ar³⁴).

shrubs are taller than in any previous station, averaging 1.8 meters, and thoroughly control the ground. The summary of a quadrat (fig. 5) follows:

	Clumps.	*Stems.*
Adenostoma	2	8
Arctostaphylos	20	55
Quercus durata	2	4
Heteromeles	1	6
Total	25	73

The bases of the stems have the large woody masses noted in station 3, and the low shrubby and herbaceous species are the same, with a number of new ones, most of which are characteristic of the nearby forest. The list follows:

Micromeria chamissonis. Dominant.
Aster radulinus. Dominant.
Rosa californica.
Trientalis europæa latifolia.
Gymnogramme triangularis.
Chlorogalum pomeridianum.
Symphoricarpos racemosus.
Galium californicum.
Pedicularis densiflora.

There is considerable litter and a moderate amount of humus. Bed rock is exposed in a few places.

STATION 7.

Descending still farther, the slope becomes steeper and we pass through a transition zone into the forest which clothes the lower part of this north-facing hillside. It is not an extensive area, the altitudinal distance covered by it being only 40 meters, but it is nevertheless well developed and typical in every way. Two stations were located in it. Station 7 is in a representative spot 12 meters

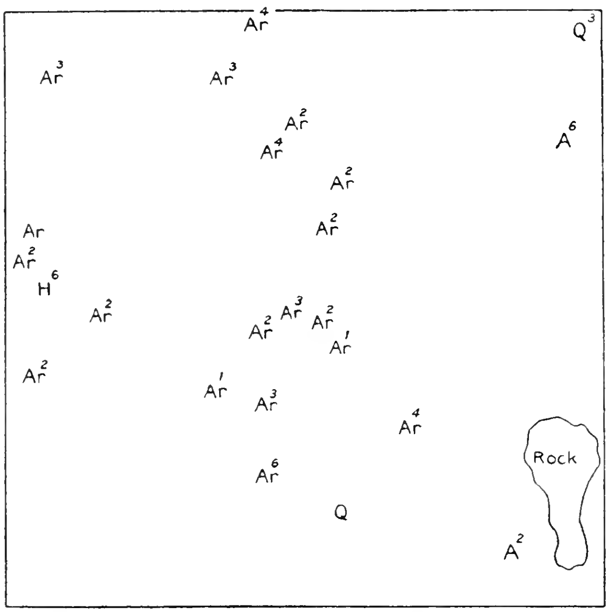


FIG. 5.—Quadrat at station 6, 5 meters square. Note likeness to station 3 (fig. 3).

above the bottom of the ravine. Since trees are the dominants here, it was necessary to increase the size of the quadrat to 10 meters on a side. This quadrat, therefore, equals in area 4 of those in other localities. A summary, as far as the dominants are concerned, is given (fig. 6):

	Clumps.	*Stems.*
Quercus agrifolia	6	6
Arbutus menziesii	2	8
Æsculus californica	2	2

The specimens of *Quercus* and *Æsculus* are all single-stemmed individuals. Those of the latter species are of little importance, being but 3.8 and 6.3 cm. in diameter. The oaks range in diameter from 3.8 to 36 cm., four being 10 cm. or larger. The eight *Arbutus* stems are in two clumps of large stump sprouts, a very common habit of the species. The diameters of the individual stems range from 10 cm. to 18 cm. The area is shaded and controlled by the three or four largest oaks and the two *Arbutus* clumps, together with other trees outside the limits of the quadrat.

If we should make a more general survey of the locality, we would find that the quadrat represents average conditions faithfully, except that another tree species, *Umbellularia californica*, occurs along the ravine-bottom and in side gulches. None of the trees are tall, the mature of all species ranging from 7 to 12 meters in

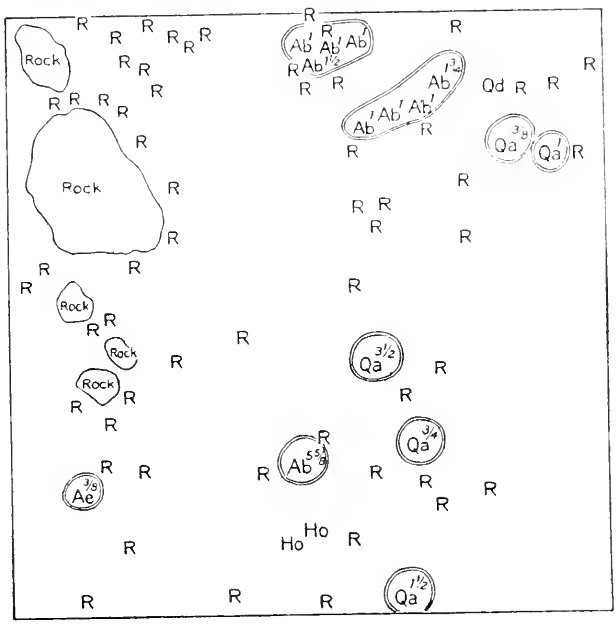


FIG. 6.—Quadrat at station 7, 10 meters square. The symbols surrounded by double lines indicate trees of the dominating stratum; the others represent the shrub stratum; the herbaceous stratum was not charted.

height. The oaks have mostly single trunks, those toward the bottom of the slope being much larger than those above. One specimen, 10 meters above the ravine-bottom, had a diameter of 8 m. The madroños mainly show the clump habit. Seedlings of oak occur, but are very rare. No madroño seedlings were found. The shade is nearly everywhere dense.

Unlike the chaparral, the oak-madroño forest shows distinct vertical zonation or layering. The dominants are the trees, and beneath them there are two subordinate strata, one composed of tall shrubs, the other of low shrubs and herbs. The first is few in species, but one of these, *Rhus diversiloba*, is abundant. Others, all relatively unimportant, are *Berberis pinnata, Holodiscus discolor ariæfolius, Rosa californica,* and *Dirca occidentalis.* With these should be included a few frequenters of disturbed areas, such as

Ceanothus sorediatus, *Eriodictyon californicum*, and *Diplacus glutinosus*, which occur in small numbers in the few openings; also, occasional wanderers from the chaparral; and finally, the young individuals of the dominant trees. The same quadrat includes the following shrubs:

Rhus diversiloba	59
Holodiscus discolor	2
Quercus durata	1

The herbaceous and ground-shrub vegetation is abundant, both in species and in individuals. The following list is nearly complete, the three most important being numbered in order of abundance:

Gymnogramme triangularis.
Adiantum jordani.
Aspidium rigidum argutum (1).
Melica imperfecta.
Luzula comosa.
Fritillaria lanceolata.
Trillium sessile giganteum.
Smilacina amplexicaulis.
Ranunculus hebecarpus.
Dentaria integrifolia.
Saxifraga californica.
Tellima heterophylla.
Potentilla glandulosa.
Psoralea physodes.
Trientalis europæa latifolia
Cynoglossum grande.
Micromeria chamissonis (2).
Pedicularis densiflora.
Galium aparine.
Galium californicum.
Symphoricarpos racemosus (3).
Hieracium albiflorum.
Achillea millefolium.

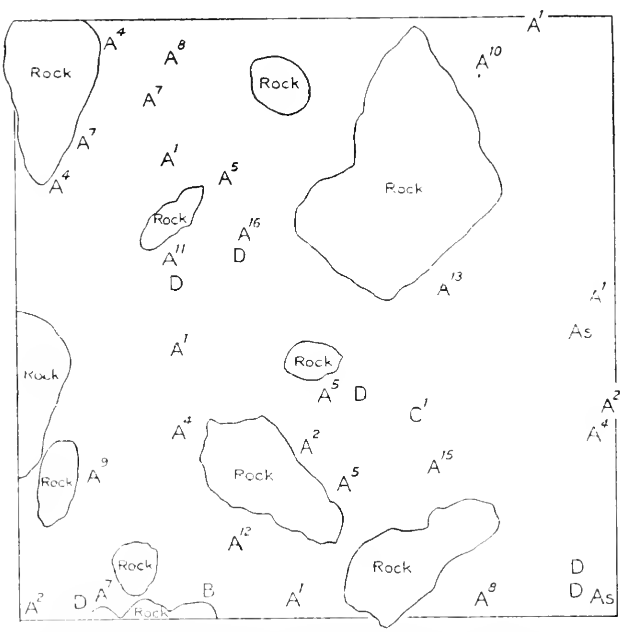


FIG. 7.—Quadrat at station 9, 5 meters square. Dominance of comparatively few individuals of *Adenostoma*.

At all times of the year this vegetation is in marked contrast to the bareness of the ground beneath the chaparral. In the spring the greenness and luxuriance are especially striking, when such plants as *Fritillaria*, *Trillium*, *Smilacina*, *Tellima*, and *Cynoglossum* are conspicuous. Litter is naturally abundant, and the soil is well supplied with humus therefrom. The occasional rock outcrops bear a fair amount of moss vegetation.

STATION 8.

This is similar to the last, but is close to the ravine bottom. *Umbellularia californica* is very important, growing in dense groups, which cast almost complete shade. Lower vegetation is almost absent in such places (although a healthy seedling of *Umbellularia* was found), but elsewhere the herbaceous element is like that described above.

STATION 9.

A sudden change of habitat, due to the sharp V-shaped bottom of the ravine, brings about a transition in vegetation that is even more abrupt than that between stations 3 and 4. Facing the oak-madroño slope and beginning in full development at the very bottom of the ravine, we find a nearly pure growth of *Adenostoma*. The shrubs are larger here than in any previous station dominated by that species, averaging 1.5 meters in height. The living and dead branches are so densely interlaced that progress even on hands and knees is almost impossible. The following summary of the quadrat (fig. 7) gives a satisfactory picture of the composition:

	Clumps.	*Stems.*
Adenostoma	29	175
Ceanothus sorediatus	1	1
Total	30	176

The one specimen of *Ceanothus sorediatus* overtops everything else. The shade is dense, considering the fact that *Adenostoma* is responsible for most of it. Ground-cover is very sparse and consists of *Aster radulinus*, *Chlorogalum pomeridianum*, and occasional small plants of *Diplacus glutinosus*. Litter and humus are scanty and the steep slope shows frequent rock outcrops.

STATION 10.

This is situated on the gently south-facing slope, 130 meters south of the last. It was chosen for special study because it was in the only chaparral area where the soil was such that excavation for water-content determination could be made in it to the desired depth. The fact that the vegetation has been slightly disturbed in consequence of its proximity to an old road does not vitiate its usefulness for this purpose. *Adenostoma* is dominant and large. *Arctostaphylos* and *Quercus durata* are both frequent, and *Q. wislizeni*, *Heteromeles*, and *Prunus ilicifolia* also occur. Because of disturbance, *Eriodictyon californicum*, *Helianthemum scoparium*, and *Diplacus glutinosus* are frequent, with quite an assemblage of small wet-season annuals. Litter and humus are scarce. The uniform sandy soil grades evenly into the bed rock, becoming too hard for excavation at a depth of a little more than a meter.

THE HABITAT.

The foregoing description, assisted by the profile (fig. 1), makes it plain that superficially the distribution of the various communities depends altogether upon the topographic factor slope. This of course is a complex of simpler factors and the present study therefore resolves itself mainly into an analysis of those factors whose variation depends upon differences in direction and angle of surface inclination.

At this point a summary of the observed angles may well be given.

TABLE 2.—*Direction and angle of slope.*

Station.	Vegetation.	Direction.	Angle.	Station.	Vegetation.	Direction.	Angle.
No. 1	Adenostoma...	S	8	No. 6	Arctostaphylos	N	30–34
2	Adenostoma...	..	0	7	Forest........	N	37
3	Arctostaphylos	N	32	8	Forest........	N	42
4	Adenostoma...	S	6–14	9	Adenostoma...	S	23–38
5	Adenostoma...	S	5	10	Adenostoma...	S	7

THE SOIL FACTORS.

PHYSICAL CHARACTER.

Samples were taken from a selected series of stations—Nos. 2, 3, 4, 6, 7, 10—these being the ones used in the study of water-content. From the first four, two each were taken, from 10 cm. and 30 cm. depth respectively. In stations 7 and 10 three depths were sampled: 10 cm., 50 cm., and 100 cm. All of these correspond with the depths used in moisture determination in each habitat. Since no differences of moment were discovered between samples from a single station, these have been combined and averaged in each case. The analyses were made by Mr. Alfred Smith, of the University of California, through the kindness of Dr. Charles F. Shaw. In the first part of table 3 the five grades of sand and gravel have been condensed into two.

TABLE 3.—*Mechanical analysis.*

Station.	Gravel.	Sand.	Silt.	Clay.	Gravel + Sand.	Silt + Clay.
2	2.30	55.71	12.66	28.96	58.01	41.62
3	2.01	78.82	2.42	16.31	80.83	18.73
4	5.58	72.08	2.01	19.92	77.66	21.93
6	1.52	76.05	2.04	20.09	77.57	22.13
7	4.61	73.21	12.54	9.34	77.82	21.88
10	1.93	81.73	7.88	8.02	83.66	15.90

It is seen that the soils in all but station 2 are closely similar, with the proportion of gravel and sand running from 77.57 to 83.66 per cent. Some, according to Dr. Shaw, would be classed as light sands and others as sandy loams. Their similarity would be assumed from field observation, the only noticeable difference being that some are a little more coherent than others. The soil of station 2 is strikingly different, having much less of the coarser grades and a correspondingly larger proportion of silt and clay, especially the latter; consequently it is sticky and heavy when wet, is unfavorable to water movement (shown by the fact that water stands in holes for many hours after a rain), and is very hard and almost rock-like when dry. Though still belonging to the sandy-loam class, it tends strongly toward clay. This physical character results in quite a different set of soil-moisture values, as will appear later, and it is therefore not surprising to find the difference in the vegetation which has been noted—a difference, however, entirely in relative luxuriance. The importance of the mechanical analysis to the present study is that it demonstrates that the soils of most of the localities studied do not differ in physical nature (excluding the humus portion), and that therefore this factor as a determinant of water-content and of vegetation has been excluded, since it is not a variable. The stations in which no analyses were made, from field observation should be grouped as follows: station 1 like station 2, 5 like 4, 8 like 7, and 9 like 10.

The same samples were submitted to Dr. Charles B. Lipman, of the University of California, for determination of humus. The depths are those noted in the last section. T indicates less than 0.1 per cent.

TABLE 4.—*Average humus content.*

Station.	Vegetation.	At 10 cm.	At 30 cm.	At 50 cm.	At 100 cm.
Nos. 2, 4, 10	Adenostoma	0.11	T	T	...
3, 6	Arctostaphylos	0.34	T	...	...
7	Forest	1.97	...	0.85	0.66

The importance of this reaction-factor in the surface layer is seen, and its penetration to a considerable depth in the forest.

THE SOIL MOISTURE.

The determinations of water-content were made in two series. In the first and more important, two stations were utilized, Nos. 7 and 10, the object being to contrast the conditions in chaparral and forest. Determinations were made weekly for a period of one year, and the series was later resumed for a few weeks for a special purpose. In the second the stations selected were the six used in the evaporation experiments and the same from which the samples for mechanical analysis were taken. This series ran parallel to the evaporation work, determinations being made at intervals of four weeks from June to April.

Series I.

Station 7 is an altogether favorable spot for the study of the forest soil. Station 10 was selected to represent the chaparral because it was the only one having a soil in which it would be possible to excavate to the desired depth. For the study of conditions surrounding the deep-rooted chaparral species, a knowledge of the water conditions in the deeper soil-layers seemed essential. Even here the deepest excavation possible did not approach the region reached by the longest roots, which, as will be shown (p. 89), penetrate the undecomposed sandstone to a considerably greater depth. Extreme shallowness of soil is general over the chaparral area in which the studies were made. It was felt that this advantage in depth of soil, which station 10 possessed, compensated for certain disadvantages—lack of slope contrast to station 7, the angle being only 7° southward, and slightly disturbed condition, due to proximity to an old road and the edge of the chaparral area.

The series was begun January 21, 1913, and continued for a total of 54 weekly observations, ending January 26, 1914. Occasionally a visit was delayed for a day or two by storms or other causes, especially in the winter of 1913-14; otherwise the program was carried through without a single break or mishap of any kind. Samples were taken in each station at three depths: 10, 50, and 100 cm. Excavations were made with a spade and samples were collected in numbered and weighed glass bottles. The sample was obtained, whenever conditions permitted, by pushing the mouth of the bottle into the freshly exposed soil-surface. When this became impossible toward the end of the dry season, especially at the lowest level, lumps of soil were cut out and pressed into the bottle, which was immediately tightly corked. The first weighings were always made within a couple of hours after digging the samples and were carried out to 0.01 gram, which is probably greater accuracy than is necessary in such determinations. The soils were dried at a temperature of 105° C., and the water-loss was computed upon the basis of dry weight.

The results have been plotted together in figure 8. The first winter was a very dry one, the total precipitation at Palo Alto being only 19.49 cm. Assuming a proportional relation at Jasper Ridge, the rainfall at the latter locality should have been 32.5 cm. The winter of 1913-14 was in great contrast to the preceding one, the precipitation at Palo Alto being 62.15 cm. and at Jasper Ridge, by actual measurement, 103.71 cm.

Taking first the three curves representing the soils of station 10, in the chaparral, we observe the following facts: The effect of rainy and dry seasons is the most conspicuous feature. The highest point reached in the first rainy season was 13 per cent, in the second

17.2 per cent. The absolute minimum was 0.5 per cent on October 31. We next observe the gradual dropping of the three lines, beginning with the end of the spring rains, continuing at a constantly decreasing rate through the dry season of summer and fall, and

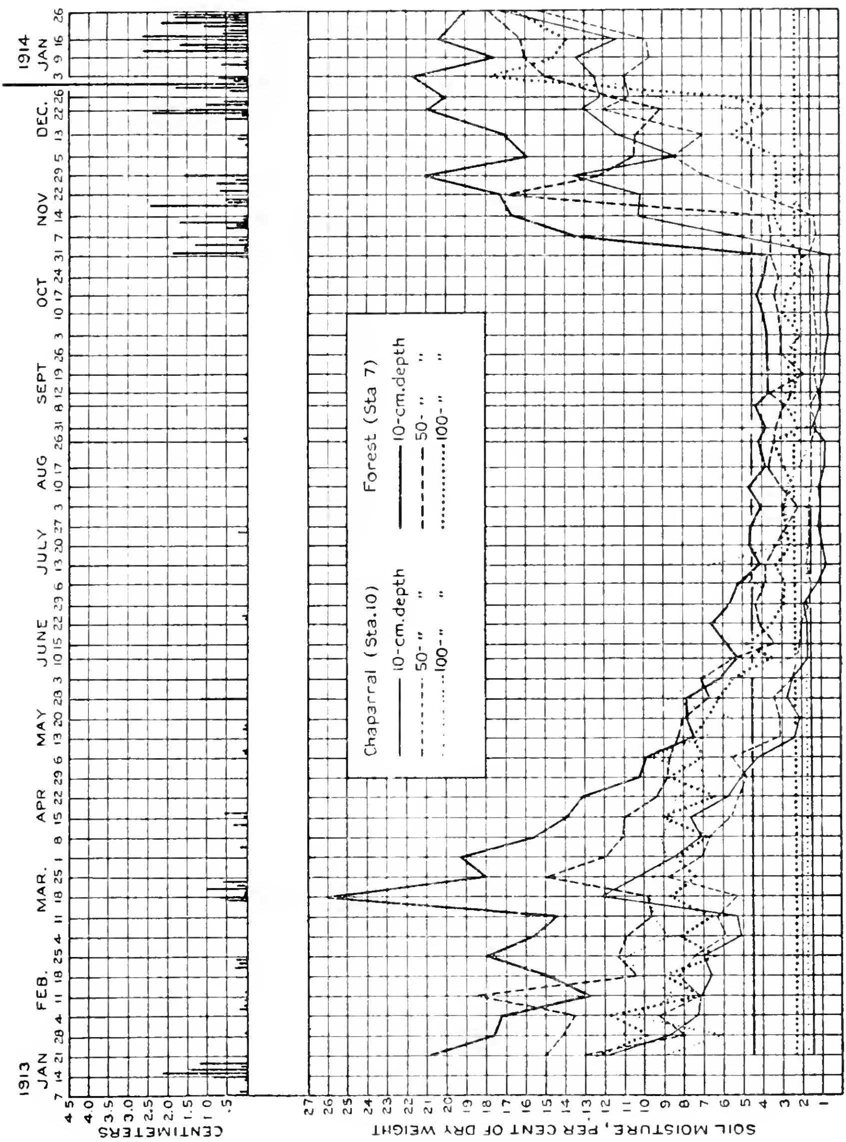


FIG. 8.—Soil moisture at weekly intervals for one year, in chaparral (station 10) and broad-sclerophyll forest (station 7), at depths of 10, 50, and 100 cm. Jasper Ridge. The wilting coefficients for the 10 cm. and 100 cm. depths have been added for each station.

thus approaching a condition of constancy. The sudden rise with the first autumn rain is the most striking single feature. Comparing the three lines, we see that the 100 cm. level had the highest water-content through most of the year, and the 10 cm. level the least. The order was suddenly reversed immediately after rains, the most striking case being at the beginning of the rainy season of 1913–14. The first rain occurred on October 31, and was a sudden, heavy shower, followed by others at frequent intervals during the month of November. From October 31 to November 6, inclusive, the precipitation at Palo Alto was 3.5 cm. Figure 8 shows that on November 7 the water-content at 10 cm. depth had risen from 0.5 per cent to 5.2 per cent and on November 14 to 10.2 per cent.

The lag in the response of the lower levels is interesting. At 50 cm. depth no effect was observable until November 22, and the increase when it came was less sudden. The water had not reached 100 cm. depth on December 5 and the rise thereafter was still more gradual. The slow penetration of the rain-water is not due to run-off, since the slope is only 7 per cent, but doubtless, in the main, to the air-filled condition of the soil. Table 5 shows roughly the rate of penetration in the two stations during this period. No important difference between the two stations is seen in this respect, and the rate of penetration was approximately uniform as far as it was followed

Table 5.—*Rate of penetration of first rains.*

	Depth of penetration in cm., first rain October 31.	
	Station 7.	Station 10.
Nov. 14	31	35
Nov. 22	50 to 60	58
Dec. 13	70 to 100+	90
Dec. 22	75	100+

Returning to station 10, we note further the tendency toward convergence of the three lines as the dry season progresses. The sudden jumps of July 13 and August 31 in the 100-cm. line are difficult to explain. They may possibly be due to encountering small masses of soil where the clay-content was above the average.

We may draw the following conclusions concerning the soil-moisture conditions in this particular chaparral station during the period studied. During the actual continuance of the rainy season there is an abundance of water at all depths. This was true even in the unusually dry winter of 1912–13. As to the following very wet season, the soil at station 10 was frequently so thoroughly saturated that the walls of the excavations continually collapsed into an almost soupy mass, making it difficult to obtain fair samples at the lowest depth. During the spring and early summer of 1913 the water-content steadily decreased, and by mid-July it had reached a point beyond which it could not drop much farther, the samples when gathered appearing as incoherent air-dry sand. From then till the first rains, three and a half months, there was a period of extreme deficiency, which is not exceeded in severity by conditions as recorded in the desert of Arizona (57). The lag of several weeks in the response of the lower strata to the first rains shows that their advent does not close the dry season, so far as the soil is concerned.

In the forest station the general form of the curve is the same, but there are nevertheless important differences. The maxima are uniformly greater than in the chaparral. Comparing the three depths, we find the relative positions of the 10-cm. and 100-cm. lines the reverse of those in the chaparral, the 10-cm. depth showing nearly always the highest water-content and the 100-cm. depth the lowest. Obviously this is to be traced to the effect of the humus on water-retaining capacity. The lines, too, during the rainy seasons, are much more widely separated than in station 10. During the dry season, however, they converge until they are as close together as those of the chaparral. The response to the first rains in the deeper levels shows a more noticeable lag than appears in the chaparral, the first certain increase at 100 cm. depth appearing on December 26, eight weeks after the earliest shower. Comparing equal depths in the two stations, we find that at 10 cm. the forest line is uniformly higher than that of the chaparral, the reasons being shade and humus. The maximum difference between them during the rainy season is 14 per cent, and the average for the rainy seasons approximately 8 per cent. During the progress of the dry season the lines converge, the average difference for the last three and a half months being 3 per cent. At 30 cm. depth the forest line is still well above that of the chaparral, but the differences are uniformly less in both wet and dry seasons. At 100 cm. no such constant differences are seen. During the first winter the chaparral soil at this depth was wetter than the forest; during the dry season and the second winter the lines cross and recross without revealing any differences of importance.

The points of greatest general import are: (1) the rather striking difference in water-content between chaparral and forest during the rainy season; (2) the convergence of the six water-content lines to minima which at the end of the dry season are not far apart.

The depletion of the water-content in every case is due to three causes. Drainage of the gravity water through the soil takes place with great rapidity during the wet season, which is proved by the fact that the ravines of Jasper Ridge contain running streams for considerable periods. After the rains have ceased, however, it can not be long before all the gravity water will have been removed from the upper meter of depth, so that this cause will no longer be operative. The second cause, evaporation directly from the soil, and the third, removal by plants, will continue throughout the dry season. Evaporation from the soil is undoubtedly higher in the chaparral habitat than in the forest, and yet the gradient of depletion, as shown by the graph, is decidedly steeper in the latter. This seems to show that the most potent cause of water-content depletion

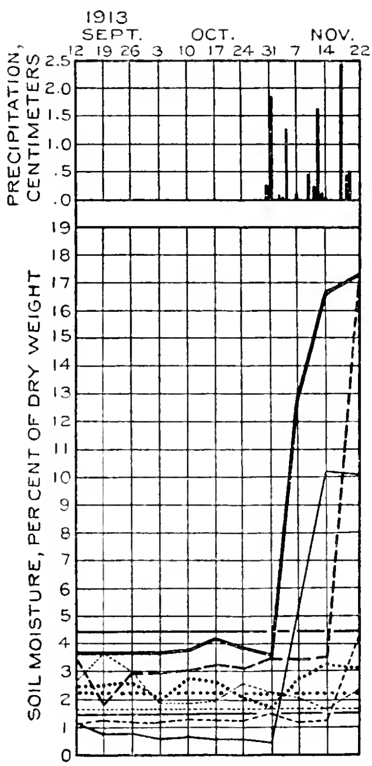


Fig. 9.—Soil moisture at end of dry and beginning of wet season, fall of 1913. Jasper Ridge. Wilting coefficients as in fig. 8.

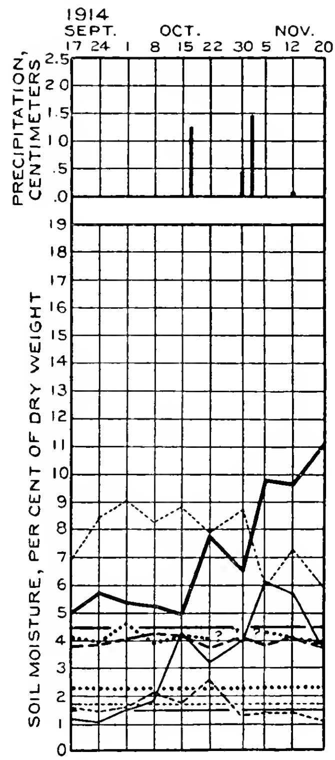


Fig. 10.—Soil moisture at end of dry and beginning of wet season, fall of 1914. Jasper Ridge. Wilting coefficients as in fig. 8.

is the vegetation itself, since where the plants are largest and most abundant, there will be the greatest drain upon the water-supply, which statement exactly fits the forest in this case. Measurements given in another connection (p. 112) show that the rate of transpiration in the same species growing in both habitats is much higher in the chaparral habitat (in the case of *Adenostoma*, forest : chaparral : : 1 : 1.92; in the case of *Arctostaphylos*, 1 : 1.69). However, it is reasonable to assume that the far greater bulk of transpiring vegetation in the forest, comprising trees of large size and luxuriant herbaceous vegetation, will much more than counterbalance the greater rapidity of the process in the chaparral.

The graph (fig. 9) shows dry season conditions after a winter of deficient rainfall (1912–13). The following winter was a very wet one, and it seemed worth while to resume the soil-moisture determinations for a few weeks during the critical period of the dry

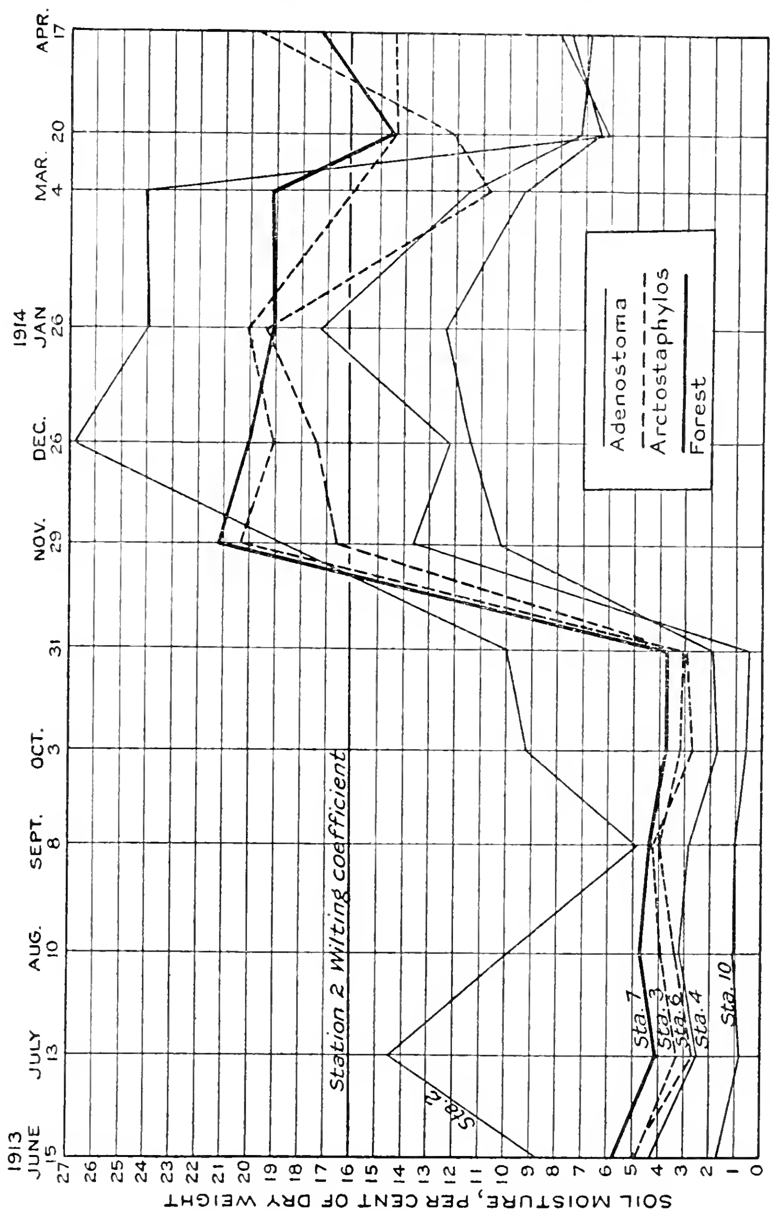


FIG. 11.—Soil-moisture at Jasper Ridge during the dry season of 1913 and the succeeding wet season; in six stations of series II, including three representing *Adenostoma* dominance and two *Arctostaphylos* dominance in the climax chaparral association, and one the *Quercus agrifolia-Arbutus* association. The wilting coefficient for station 2 has been added.

season following. The two graphs side by side (figs. 9 and 10) give the minima shown in table 6. This shows that there are very perceptible differences in water-content at the critical periods

TABLE 6.

Years.	Chaparral.			Forest.		
	10 cm.	50 cm.	100 cm.	10 cm.	50 cm.	100 cm.
1913	0.5	1.1	1.7	3.7	1.9	1.8
1914	1.1	1.1	5.9	5	3.7	3.9

following winters of deficient and abundant rainfall, and that these differences appear especially in the deeper soil-layers. In the chaparral, at 100 cm. depth, the minimum percentage after a wet winter was more than three times that of the preceding season; at the corresponding forest depth the percentage was more than twice that of 1913.

SERIES II.

This series was carried out at the same six stations that were used for the evaporation studies, and during the same period (June 15, 1913, to April 17, 1914). There were thus provided three examples of *Adenostoma* chaparral (Nos. 2, 4 and 10), two of *Arctostaphylos* chaparral (Nos. 3 and 6), and one of forest (No. 7). The samples were taken at intervals of 4 weeks, and in stations 2, 3, 4, and 6 at two depths—10 cm. and 30 cm. In stations 7 and 10 the figures from Series I were used, the 50-cm. depth being considered as parallel to the 30-cm. depth in the other stations. In figure 11 the results for the 10-cm. depth are compared.

The most striking feature is the line representing station 2, the highest in water-content and yet the poorest in vegetation. The explanation of this apparent paradox is found in the mechanical analysis and wilting coefficient. The sudden changes in water-content without apparent reason—e. g., the sharp crest on July 13 and the sudden drop after March 4—are perhaps due to local soil differences, small masses of unusually high or unusually low clay-content. The other two *Adenostoma* stations are consistently the lowest and the forest is the highest. Between forest and *Adenostoma* chaparral are the two *Arctostaphylos* stations. In figure 12 all stations of each type, both depths, have been averaged, station 2 being omitted. The daily precipitation for the period is also added. The *Adenostoma* community is decidedly the lowest, and the forest is highest most of the time, though the *Arctostaphylos* community is not far below. The close approach of all the lines during the dry season and their separation during the wet season (seen in Series I) are evident here also. In general, Series II confirms the results obtained in Series I and adds data for the *Arctostaphylos* community, which is seen to be intermediate in water-content between the other two.

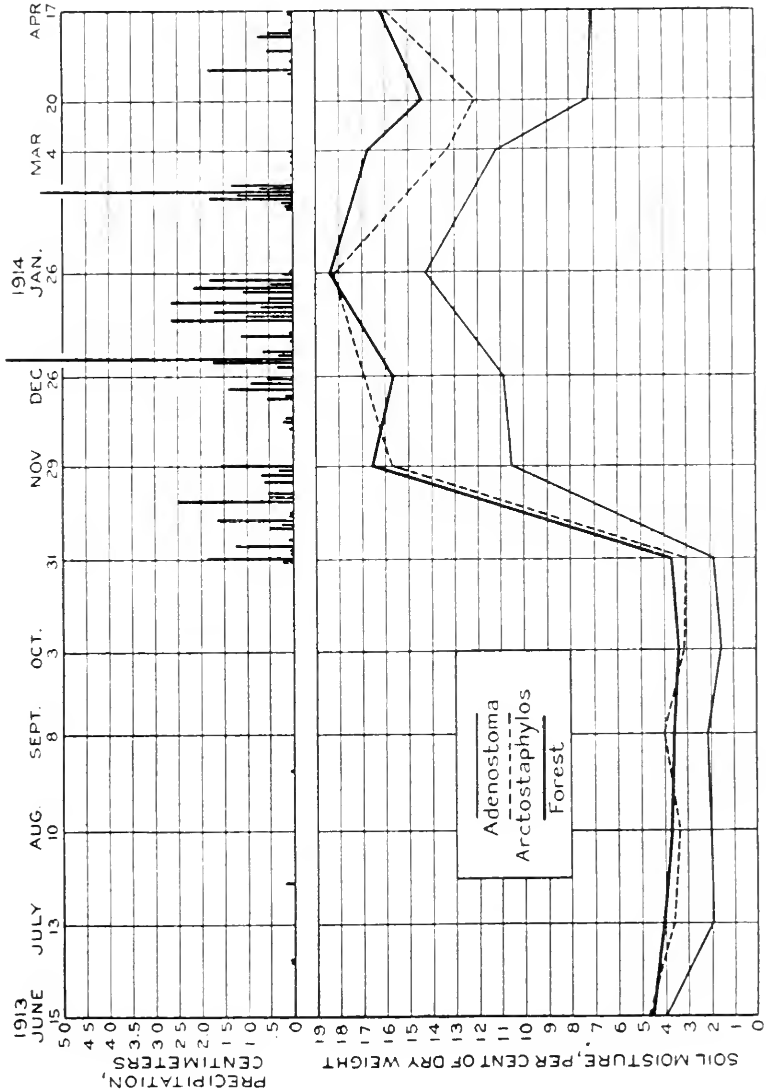


FIG. 12.—Soil-moisture in the stations of fig. 11, each representing the average of two depths and all stations for a single community. Station 2 has been omitted, and the daily precipitation for the period added.

Water-retaining capacity.—The reasonable way to compute water-retaining capacity is upon the basis of dry volume of soil. The same is true of water-content, but as yet it is not feasible to make moisture determinations in extensive series on the basis of volume. For the sake of uniformity, therefore, it is convenient to express the water-retaining capacity in terms of dry weight as well as of dry volume. The method employed was the one which has been in general use of late. Circular pans were made having bottoms of perforated metal, with sides 1 cm. high and of such an area that the capacity, when the soil was smoothed off level with the top, would be 100 c. c. The bottoms were covered with cheese-cloth. The soils were all prepared—pulverized and compacted—as nearly as possible in the same way, and the pans, filled level full, were stood in shallow water to permit absorption. After saturation was complete they were allowed to drain until all the gravity water had passed off. The percentage of water retained was then calculated upon the basis of dry weight and also of dry volume. In each case the average of five tests was used. The shortcomings of the method are fully realized, prominent among them being the unnatural condition of the soils when tested. The results, however, although they do not give a true picture of the behavior of a given soil under natural conditions, do give data whereby fair comparison may be made between different ones. Samples were taken from the three depths in stations 7 and 10 for comparison of conditions in forest and chaparral, and from station 2 because of its peculiar qualities.

TABLE 7.—*Water-retaining capacity, percentages.*

Station.	At 10 cm.	At 10 to 30 cm.	At 50 cm.	At 100 cm.	Average all depths.	Ratio.
By dry weight:						
No. 10, chaparral..	20.6	....	17.9	21.4	20	1
No. 7, forest......	30.5	....	24.9	16.3	23.9	1.20
No. 2............	....	46.4	....	....	46.4	2.32
By dry volume:						
No. 10, chaparral..	38.5	....	36.7	39.4	38.2	1
No. 7, forest......	49.3	....	47.3	32.5	43.0	1.13
No. 2............	....	71.4	....	....	71.4	1.87

Considering the dry-volume figures, which give the truest picture of the soil qualities, we note that there are no differences of importance among the various depths in station 10. The high water-retaining capacity in station 7 at 10 cm. depth is plainly due to the large humus content. The high figure for station 7, 50 cm. depth, as compared with the low one for 100 cm., is difficult to explain. Mechanical analysis offers no clue; nor does humus content, since 50 cm. and 100 cm. are more like to each other than to 10 cm. depth. Station 2 shows striking originality in this feature as in others, and the reason is plain—the high percentage of clay and silt. Summarizing, we find that the comparative water-retaining capacities of stations 10, 7, and 2, representing chaparral, forest, and a particularly unfavorable chaparral station, may be expressed by the ratio 1 : 1.13 : 1.87.

A second series of determinations was made at a later time. The percentages are somewhat higher, but the relative values are very similar in most cases, which is the important thing. The series given here is the more valuable, since the soils used were composites of many individual samples.

Wilting coefficient.—The method developed by Briggs and Shantz (15) was followed, and the soils to be tested were brought from Jasper Ridge to the University of Minnesota. The experiment was carried on in the university greenhouse, in a room where the relative humidity averages 30 to 40 per cent during the middle of the day. An atmometer was kept in operation close to the jars during most of the period of growth and wilting. The average daily evaporation recorded, reduced to the usual standard, was 10.2 c. c. The extremes were 14.7 c. c. and 3.1 c. c. Glass tumblers were used for containers and a constant soil temperature was maintained by immersing them almost to the top in slowly running water. Kubanka wheat, obtained through the kindness of Dr. Briggs and Dr. Shantz, was used as the indicator plant.

The constant termed the "wilting coefficient" has been variously interpreted. The latest and most reasonable conception, due to Shull (82) and Moore (65), is that it is purely a function of the soil, "a point in the water-content of the soil at which the water practically ceases to move along the film (on the soil particle), no matter how sharp the gradient at the edge of the film," and not a matter of "balance between the 'back-pull' of the soil and the pull of the plant." If this be true, one plant is as good as another for indicator use, and Kubanka wheat will furnish just as serviceable results as would *Adenostoma*. This is fortunate, since difficulty has been encountered in bringing about germination of the chaparral species under artificial conditions. The one chief essential to success seems to be the maintenance of uniform environmental conditions during the period of the experiment, especially those affecting the evaporation-rate. It must never be forgotten that the wilting coefficient is the ultimate point at which plants *must* wilt, but that under certain conditions wilting *may* take place before that point is reached. Its usefulness in the investigation of different soils with regard to their effect upon plant life is obvious.

Comparison was made primarily between the soils of two stations, Nos. 7 and 10, representative of forest and chaparral respectively. In each case two depths were considered, 10 and 100 cm. Station 2 was added because of the interesting singularity apparent in its other characteristics. The figures in table 8 are each an average of seven unimpeachable determinations.

The figures are about what one would expect after study of the physical character of the soils and their water-retaining capacities.

Station 10, almost a pure sand, has a very low wilting coefficient, with no difference of moment between the two depths, since the surface layer has but a very slight admixture of humus. In station 7 the effect of surface humus in raising the wilting coefficient is very evident. In station 2 the large percentage of silt and clay is responsible for a strikingly high figure.

TABLE 8.—*Wilting coefficient in stations 10, 7, and 2.*

Depth.	Station 10.	Station 7.	Station 2.
	p. ct.	*p. ct.*	*p. ct.*
10 cm...	1.5	4.5	16.1
100 cm...	1.7	2.3	....

It has been customary to draw a line to indicate the wilting coefficient upon the graph representing the seasonal march of soil-moisture. Accepting the interpretation of the wilting coefficient presented by Shantz and Moore, we are justified in drawing this line, and in assuming that, when the water-content line falls below that of the wilting coefficient, the vegetation can extract no moisture from the soil. Referring to figure 8, then, we find that in station 10 (chaparral) there was at 10 cm. depth no available water from July 1 to November 1. At 100 cm. depth the water-content line, though it is not far above the wilting coefficient, actually touches it but once. In station 7 (forest) conditions at 10 cm. depth were only slightly better than in station 10, water-content and wilting coefficient lines both being relatively and equally high. The period of unavailable water was shorter by the first two weeks of July. At 100 cm. depth conditions were actually less favorable than in station 10, since three times the water-content line descends below that of the wilting coefficient. With regard to the relation between water-content and wilting coefficient, it would seem that there is no striking difference between stations 10 and 7; that soil-moisture conditions, as indicated by these two factors, are about equally severe during the critical period.

The dry season of 1913 was of unusual severity. That the conditions recorded are extreme is indicated by figure 10, presenting the soil-moisture in relation to the wilting coefficient at the critical period of 1914, which followed a very wet winter. Except for station 10, at 10 cm. depth, the water-content was everywhere well above the wilting coefficient, and the abundance of available water at 100 cm. depth in station 10 is noteworthy. Very likely the average condition is somewhere between the extremes of 1913 and 1914, but the special importance of seasons of unusual severity (like that of 1913), which recur every few years with tolerable regularity, is fundamental.

In station 2, the constantly high water-content is rendered ineffective by the high wilting coefficient. At 10 cm. depth, during the period from June 15, 1913, to April 17, 1914, the soil furnished available water only from November 1 to April 1. It seems unnecessary to seek further for the explanation of the poverty of the vegetation in that station and its vicinity.

The Soil Temperature.

In making determinations of soil temperature, the simplest method seemed the best—the plunging of a chemical thermometer into the freshly cut surface at the time of taking water-content samples. During the dry season it was found necessary at the lowest level to bore a hole with a small auger. The observations were made in the two stations of water-content Series I, at all depths used in that series. They were begun March 25, 1913, and with a few minor interruptions continued to January 26, 1914, the closing date for the soil-moisture work. During much of the period the temperature of the surface was also observed, in shade in station 7 and in sun and shade in station 10. In these cases the bulb of the thermometer was covered with a thin layer of soil or litter. The results are plotted in figure 13.

The first point to note is that during the dry season the soil temperatures in the two stations are widely different, the three lines representing station 10 being all of them regularly below those of station 7. With the arrival of the wet season they all descend and at the same time converge, the differences between them almost disappearing. This is exactly the reverse of the soil-moisture's behavior, where convergence takes place in the dry season. It is due of course to the greatly increased water-content of both soils. The surface temperatures, naturally the highest in each station through most of the period, show the same tendency, and in the case of station 7 the line actually drops below those representing the subterranean temperatures.

Comparing the lines of a single habitat, we find that in station 7, during the dry season, the temperatures vary inversely with the depth, the order being, from highest to lowest, surface, 10 cm., 50 cm., 100 cm. During the wet season the order is roughly the reverse, the order most of the time being 100 cm., 50 cm., 10 cm., surface. In station 10 the case is the same, except that the shaded surface and 10 cm. lines do not greatly differ, because of the lack of cover, and in the wet-season portion the lines do not hold constant relative positions. In both stations the greatest fluctuations occur at the surface and at 10 cm. depth, and the greatest uniformity at 100 cm. depth.

THE ATMOSPHERIC FACTORS.

LIGHT.

On August 17, 1917, a series of observations was made to determine the relative light values at the different stations. The apparatus used was the Clements photometer. The observations were made as rapidly as possible in the course of a trip over the trail from station 1 to station 10. The first was made at $2^h\ 30^m$ p. m. and the

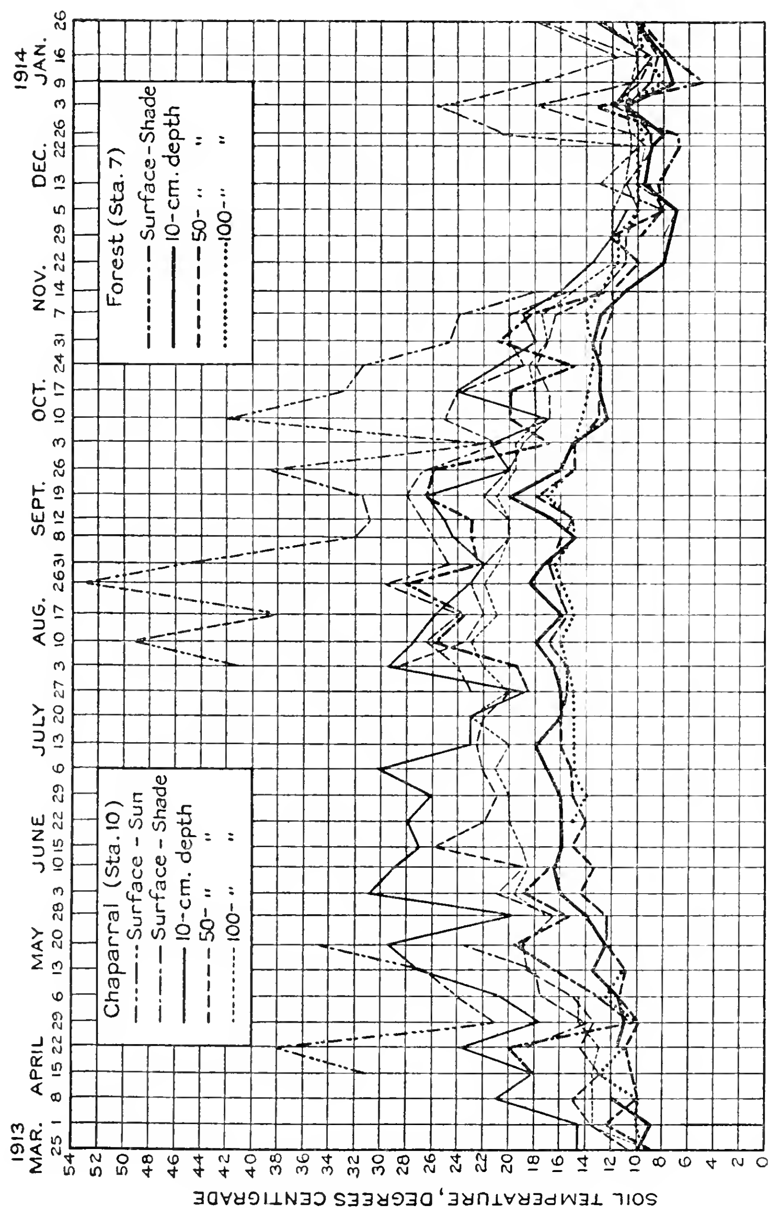


FIG. 13.—Soil temperature at weekly intervals during the dry season of 1913 and part of the succeeding wet season, in chaparral (station 10) and broad-sclerophyll forest (station 7), at depths of 10, 50, and 100 cm. Jasper Ridge.

last at $3^h\ 15^m$. Those toward the end are therefore comparatively a trifle too low. In the computation the highest value obtained (at station 5) is taken as unity and the others are reduced to decimals in proportion. In the observations of sun intensity the instrument was pointed directly toward the sun. In the spotty shade of the chaparral it was moved about continually during the exposure, so that an average figure was obtained.

TABLE 9.—*Light intensity at stations 1 to 10.*

Stations.	Sun.	Shade.	Stations.	Sun.	Shade.	Summary.			
							Sun.	Shade.	Proportion.
No. 1	0.94	0.20	No. 6	0.69	0.10	Adenostoma. . .	0.84	0.17	100 to 20
2	.75	.17	7	.56	.07	Arctostaphylos	.69	.07	100 to 10
3	.69	.04	8	. . . .	.05	Forest.	.56	.06	100 to 11
4	.75	.21	9	. . . .	.11				
5	1.00	.23	10	.75	.07				

The great differences in the direct sunlight intensities are apparently due to differences in amount of reflected and diffused light, the chaparral stations, with much bare light-colored soil naturally being the highest, and the forest, with dark soil and much vegetation, the lowest. The shade differences are less than might be expected.

TEMPERATURE.

In the matter of atmospheric temperature there is an unfortunate shortage of data. Isolated observations of so variable a factor, even though numerous, are of little value. The thermograph is the only satisfactory apparatus for habitat study, and no thermographs were available for the work. Some knowledge of comparative temperature values during the dry season may be gained from two series of observations (table 10), obtained during trips over the trail connecting the stations. The first was made during the middle of the day, the second between 3 and 4 p. m. The readings were made from the dry bulb of the cog psychrometer in the process of measuring relative humidity.

The outstanding feature is the uniformity of temperature. No differences of moment occur between any of the stations, nor between sun and shade. The latter would, of course, not be true if the sun had been allowed to shine on a stationary bulb. The probable effect in such a case is roughly indicated by the high sun temperatures recorded in the surface lines of the soil temperature graph (fig. 13). As the air readings stand, the shade temperature in the *Adenostoma* stations is in nearly every case higher than the sun temperatures, while in the other stations the reverse is true. The reason in the former case is not clear.

The maxima during the dry season would often be considerably higher than those recorded here. Even in winter the day temperatures are frequently quite high. Frosts are rare and slight. During the winter of 1913–14 no atmometers were broken from this cause—and these instruments are very sensitive to that danger.

TABLE 10.—*Atmospheric temperature.*

	July 4, 1916.		Aug. 16, 1917.	
	Sun.	Shade.	Sun.	Shade.
Station No. 1...	27.5	30	22.8	24.4
2...	25	28.5	22.5	23.9
3...	27.7	25.5	21.7	20.3
4...	30	29.5	23.6	23.4
5...	29.5	30	23.9	25.0
6...	28	25.7	22.8	21.1
7...	27	26	20.8	18.9
8...	28	25.6	20	19.4
9...	26.3	27.5	21.7	20.6
10...	26.6	26	20.6	21.7
Summary:				
Adenostoma...	27.5	28.6	22.5	23.2
Arctostaphylos.	27.8	25.6	22.2	20.7
Forest........	27.5	25.8	20.4	19.1

WIND.

I have no data for Jasper Ridge, but a statement as to the surrounding region as a whole will be of value. Throughout the Santa Cruz Peninsula and northern Santa Clara Valley, except where topography produces local differences, the prevailing direction of wind is northwest. During the dry season this is almost universally true. During the wet season the direction is much more variable. Northwest winds are still the commonest, but the severe storms that bring the rains are usually accompanied by gales from the southwest. The north-facing slopes, therefore, receive most of the dry summer winds, while the south-facing slopes receive the full force of the rain-bearing winter gales. That the former may be very severe in their effects I have shown in another paper (23, p. 187). The actual vegetation cover of the north- and south-facing slopes is evidence that in general the prevailing winds are not important as locally controlling factors.

THE ATMOSPHERIC MOISTURE.

Rainfall, cloud, and fog.—These topics have already been treated (p. 31). They are of interest in consideration of the locality as a unit, but have little influence upon the distribution of the plant communities as determined by slope exposure.

Relative humidity.—The effects of relative humidity upon vegetation are included when the evaporating power of the air is measured, as are also in part the effects of temperature, wind, and light. The two series of observations shown in table 11 are of interest, however, in illustrating the values of this simple factor in the various stations. The readings were made with a cog psychrometer, breast-high, except where dense chaparral made a lower level necessary.

TABLE 11.—*Relative humidity, percentages.*

	July 4, 1916.		Aug. 16, 1917.	
	Sun.	Shade.	Sun.	Shade.
Station No. 1...	48	43	53	51
2...	57	46	59	54
3...	48	49	60	60
4...	44	42	56	52
5...	42	39	54	48
6...	45	49	57	59
7...	49	48	61	66
8...	45	47	62	66
9...	46	42	60	63
10...	54	48	63	60
Summary:				
Adenostoma...	48.5	43.3	57.5	54.7
Arctostaphylos.	46.5	49	58.5	59.5
Forest........	47	47.5	61.5	66

The percentages given in table 11 do not approach to what we are accustomed to think of as xerophytic values. It may be that they do not represent average dry-season conditions, though there is ample reason in the proximity of the bay and the ocean for relatively high humidity. Other chaparral localities would certainly show a much lower average. The sun humidities in the *Adenostoma* habitats are higher than those in the shade; in the other stations the order is reversed.

Evaporation.—Observations were made by means of the Livingston cylindrical porous-cup atmometer, standardized at the beginning and end of their use by the Plant World Company. For dry-season study instruments were set out in all the stations except No. 10, two per station, one at the level of the ground, and one near the top of the vegetation in the region of most abundant foliage. The instruments at the ground-level were set in small excavations, so that the tops of the porous cups were about 2 dm. above the surface. Those at the upper levels were set upon posts of proper height, ranging from 0.7 meter in station 1 to 2.5 meters in station 6. In the forest stations, No. 7 and 8, it was necessary to construct wire trolleys running to the tops of trees, so that the instruments could be lowered for measurement.

Considerable trouble was encountered by reason of the depredations of thirsty animals, and several of the surface cups were destroyed, so that the lower series is incomplete. The dry-season study was carried on from June 8 to October 17, 1913, and readings were taken at weekly intervals, with a few irregularities. For the investigation of rainy-season conditions, stations 3, 4, and 7 were

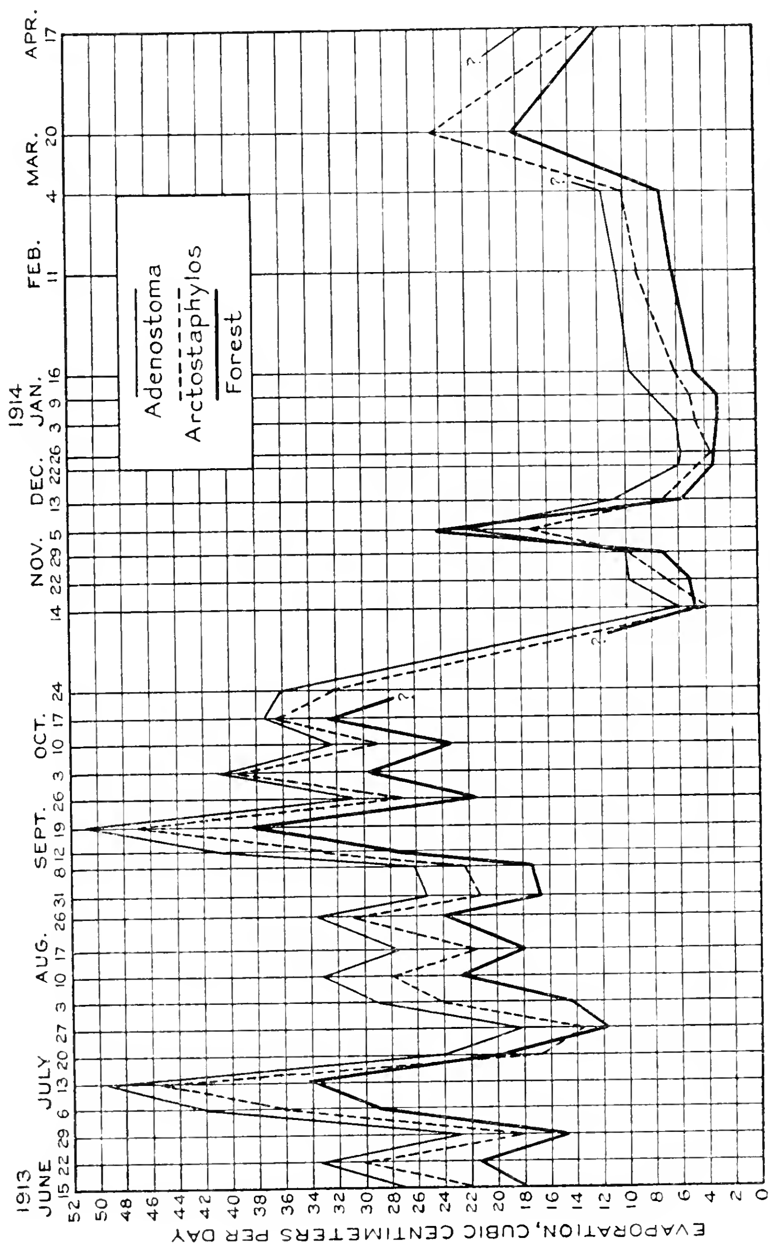


FIG. 14.—Evaporation at Jasper Ridge during the dry season of 1913 and the succeeding wet season, for *Adenostoma* and *Arctostaphylos* dominance in the climax chaparral association, and for the *Quercus agrifolia-Arbutus* association, stations 2, 3, and 7, respectively.

selected, representing the *Adenostoma*, *Arctostaphylos*, and forest habitats, and rain-correcting atmometers were substituted for the ordinary kind. The surface instruments were surrounded with chicken wire, which proved an adequate defense. Readings were taken weekly until the close of the soil-moisture observations on January 16, 1914, and at intervals of approximately four weeks

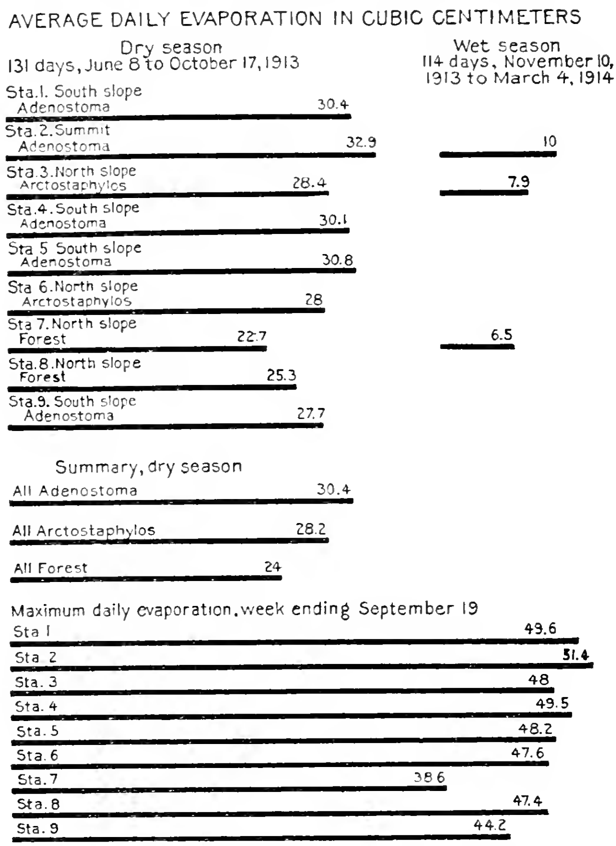


FIG. 15.—Average daily evaporation in cubic centimeters in stations 1 to 9 at Jasper Ridge, for the dry season of 1913 and the succeeding wet season; also the maximum daily rate (week ending Sept. 19).

thereafter until April 17, when the series was closed. We thus have records of one complete dry season, following a winter of deficient rainfall, and of one complete wet season—an unusually rainy one—fair samples of extremes in both directions. The dry-season series is complete for nine stations at the upper level and incomplete for the lower; the wet-season series is practically complete for the representative stations at both levels.

The results have been summarized in three figures. In figure 14 the upper-level series is used, and the water-losses for three representative stations (Nos. 2, 3, and 7) are given. These, as presented, denote the average daily evaporation in cubic centimeters for each observation period, reduced to the official standard maintained by the Laboratory of Plant Physiology of Johns Hopkins University. The conclusions may be very simply stated. The high rate of evaporation for the dry season and the low for the rainy season are immediately evident. A rainless period in December caused a sharp rise. The relative positions of the three lines are maintained throughout the period of observation almost without change, the *Adenostoma* habitats having the highest rates and the forest the lowest. The absolute maximum attained was 51.4 c. c. in station 2, *Adenostoma* chaparral, for the week ending September 19. This period included some of the hottest days recorded for the region. The absolute minimum was attained on January 9, 3 c. c. daily evaporation for the period of 6 days preceding.

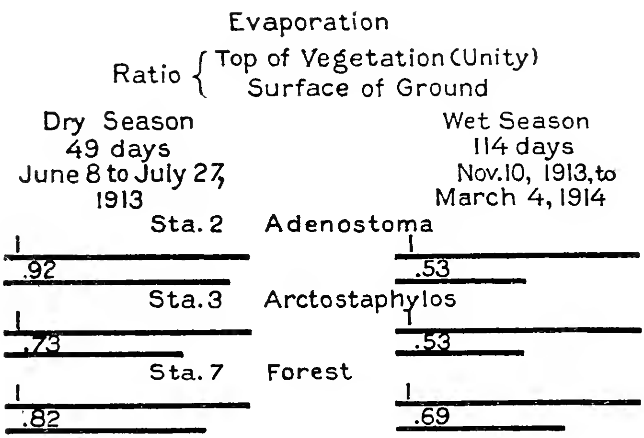


FIG. 16.—Ratio between evaporation at top of vegetation and at surface of ground, in three representative stations at Jasper Ridge.

In figure 15 the average daily evaporation for each station is given, for both wet and dry seasons, readings from the upper series of instruments being used. During the dry season the *Adenostoma* stations have regularly the highest rates. Station 2, located on the topmost point of Jasper Ridge, exposed to winds from every direction, naturally has the highest of all. Stations 1, 4, and 5, on gentle south-facing slopes, come next, and station 9, on the steep south-facing slope of an abrupt ravine, is last, falling slightly below the *Arctostaphylos* stations. The latter (stations 3 and 6) are closely alike, and fall between the *Adenostoma* and the forest stations, but nearer the former. The forest stations are decidedly below the others. Evaporation during the wet season averages about 30 per cent of the dry-season rate in the stations studied. The figure also shows rates of evaporation during the most extreme conditions of the year. The figure for station 8 seems abnormal.

Figure 16 presents the ratio between evaporation at the top of the vegetation and at the surface of the ground. Stations 2, 3, and 7 were selected, since they were continued through both wet and dry seasons, and the average daily losses for the period are used in computing the ratios. During the dry season the rates at the two levels did not differ very greatly, while during the wet season the differences were considerable, especially in the chaparral stations. This suggests that during the latter period there is a surface stratum of moist air due to evaporation from the saturated soil, and that the contrast between it and the upper air layers is greater in the chaparral stations than in the forest because of freer circulation.

DISCUSSION AND CORRELATIONS.

It is very easy and pleasant to describe the vegetation of a locality, to mark it out into communities, and to name the dominant and secondary species thereof, and even to present quadrats of the same. It is not so easy completely to analyze the habitat. With our present methods of investigation certain factors elude us almost altogether, and much of the data, even when obtained, is difficult to utilize. It is most difficult satisfactorily to link vegetation and the measured factors of the habitat in the relation of cause and effect. The present chapter has so far been devoted to description of vegetation and analysis of habitat. Some correlations of the two will now be attempted.

THE BROAD-SCLEROPHYLLS AND THEIR HABITAT.

After the analytical treatment that has preceded, it is proper first to synthesize the various elements into a whole, to characterize the broad-sclerophyll habitat as a unit, so far as we fairly may from the data in hand. Afterward it will be in order to consider habitat differences and community differences and their correlation.

To describe the broad-sclerophyll habitat in the large is merely to describe the climate of California west of the Sierras and its effects upon the soil factors. Emphasis must be placed upon the complete seasonal march of the factors, since vegetative activity of some sort and degree may here take place the whole year through.

Of direct and fundamental importance is soil-moisture. Its great abundance during the winter months makes ample provision for growth during that time. The supply is made more completely available by the low air-temperature and low evaporation-rate during the period. The cessation of the rains at some time during the spring is followed by gradual depletion of the water-content, due to failure of the renewal supply, gravity drainage, evaporation from the soil, and absorption by the vegetation itself. These partial causes will vary in importance in various places. In a region of relatively heavy rainfall, the dry season is likely to be shorter and the supply will dwindle less rapidly. A soil with a high water-retaining capacity will lose less through gravity. If the evaporation-rate is high, more will be lost thereby, and forest vegetation will extract a far greater quantity than will scrub. But whatever the difference in rate due to these separate elements, the depletion goes on, and the water-content approaches the wilting coefficient. In some places at least, and in some years, it actually drops below for a considerable period. The Jasper Ridge observations demonstrate this; moreover, the general conditions of moisture here are much less severe than in other regions where broad-sclerophylls are even more thoroughly in control. When the autumn rains finally arrive there is still, in some soils at least, a period of several weeks before the water forces its way into the deeper layers of the air-dry soil. The importance of this delay is lessened somewhat by the fact that much of the root system is contained within the first half-meter of depth. There is probably but small delay in the production of new absorption apparatus from the old dormant roots, once the moisture touches them.

As the store of soil-moisture decreases, the evaporation-rate rises and water-loss from the leaves must increase. Thus the water-balance is affected unfavorably at both ends at the same time, and the late summer and early autumn, therefore, constitute the time of greatest danger. The deeply penetrating roots and the effectively guarded leaves are the answer.

Air-temperature and, in response, soil-temperature, at a minimum during the months of abundant moisture, rise as water-content decreases. This combination is altogether unfavorable for vegetative activity. When moisture is abundant, the low soil-temperature makes absorption difficult and root-growth slow, and the low air-temperature is unfavorable to photosynthesis and the other growth activities. When the soil-temperature is favorable for root-growth and absorption, the water-content is scanty or negligible. When air-temperature is favorable to rapid photosynthesis, the water supply necessary to that process and to vigorous growth is insufficient. High temperature is now itself a danger, in that it raises the evaporation-rate and thus increases the depletion of the scanty moisture supply, both in plant and soil.

The seasonal development of the broad-sclerophylls is accurately adjusted to the peculiar seasonal march of the factors just outlined. With the beginning of the heavy rains (usually December, sometimes earlier or later), growth starts in most of the species. The history in detail presents many variations. For instance, *Arctostaphylos* flowers immediately from buds already formed, then proceeds to put forth new leaf-shoots, which terminate with next year's flower-buds. When these are fully formed (about May), growth for the year practically ceases. In *Adenostoma* the procedure is exactly the reverse. This species begins its activity with the formation of its vegetative shoots, and its flowers, borne on these, open in June and close the period of active growth. All agree in making the fullest utilization of the relatively short period when both moisture and temperature conditions come nearest to combining for the general good, i. e., in the spring months, when soil-moisture is still abundant and air and soil temperatures are on the increase. April, in the Palo Alto region, is the month of greatest vegetative activity among the broad-sclerophylls and other types of plants as well. An additional advantage which many of the former show at this time is the possession of an increased photosynthetic apparatus, since the last year's leaves have not yet fallen and the new ones have reached or are approaching maturity. It is doubtless at this period that the superficial roots described on page 91 have their greatest extension. A glance at figure 8 will reveal the interesting fact that it was in April that the soil-moisture suffered the most rapid depletion—a fact that may reasonably be referred to the abundant use of water by the vegetation at this time.

Soon after the period of maximum activity, the decreasing water-supply makes a limitation of growth inevitable and necessary, and it is surely more than a coincidence that a number of the species drop their oldest leaves rather regularly during the month of June. This phenomenon is sometimes so constant and definite that the chaparral may take on a distinctly yellowish hue for a few days, resuming its normal tone after the old leaves have dropped off. The same is strikingly true of the broad-sclerophyll tree *Arbutus*, which passes through a period in June when dead leaves are its most conspicuous feature. It is of interest to note further that *Æsculus californica*, not an evergreen, has a corresponding habit, dropping its leaves gradually during the summer, apparently as a response to the decreasing water-supply, until it is often nearly leafless before autumn. After the period of leaf fall the broad-sclerophylls enter a state bordering upon dormancy, growing very little, merely maintaining themselves through the scanty supply of water absorbed by the few roots that penetrate the deeper soil layers.

That water lack is the reason for the stoppage of growth activity is shown by the behavior of stump sprouts. If the aerial portions of a shrub are removed during the dry season, even in the most severe part of it, sprouts are immediately put forth which grow with amazing rapidity. On Mount Tamalpais, three weeks after a severe fire, I found sprouts of scrub oak 45 cm. high. Visiting the scene of the Ojai Valley fire of June 1917, six weeks after the event, sprouts of 90 cm. were found. In such cases the water-supply of a whole clump of shoots is suddenly concentrated upon a few small sprouts. Moisture and temperature are both favorable to the utmost, and strikingly rapid growth is the result.

The meaning of the evergreen sclerophyll is plain enough when the seasonal factor-march is thus considered. It is a compromise which enables the plant to meet the lack of agreement in time between

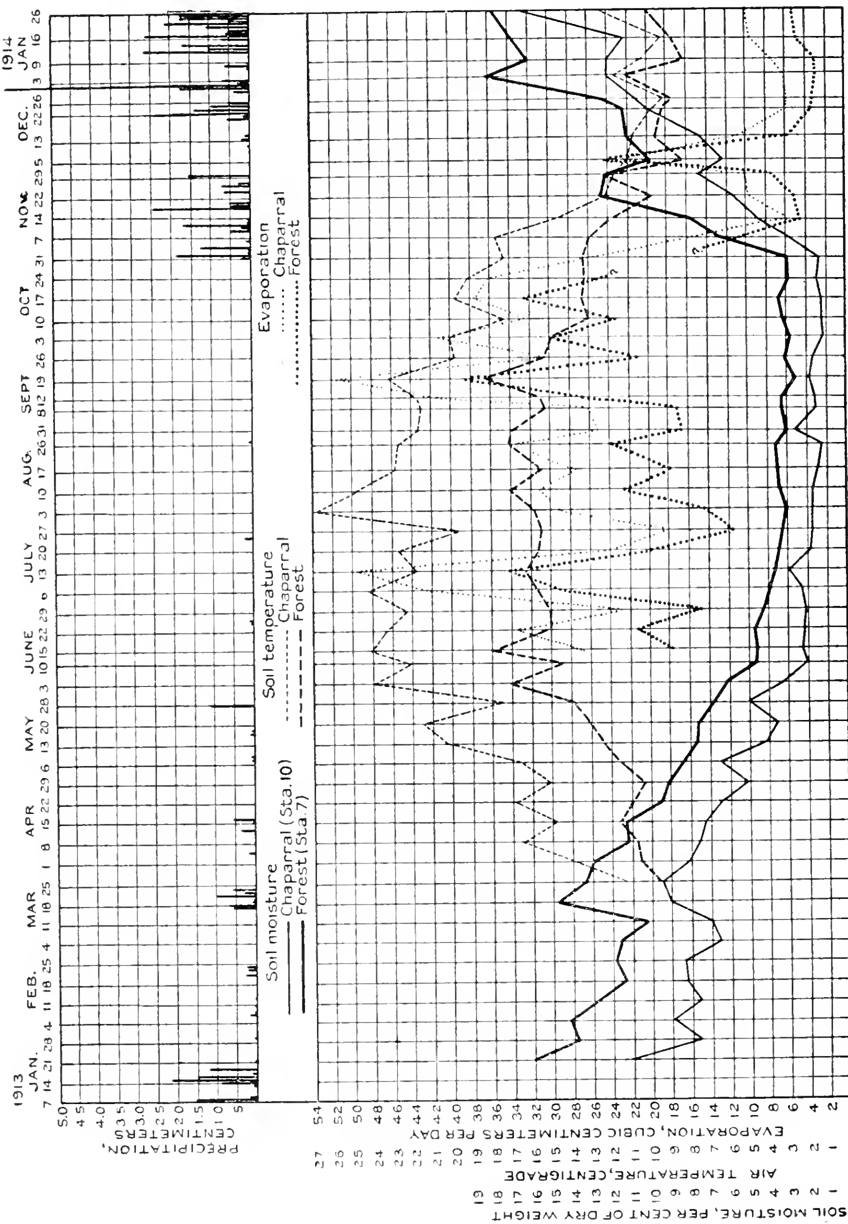


FIG. 17.—Summary graph of habitat factors at Jasper Ridge, for chaparral (station 10) and broad-sclerophyll forest (station 7): rainfall, soil-moisture, soil-temperature, evaporation.

moisture and temperature optima. The prominent cuticle and the other features that are effective in limiting water-loss enable the plant to exist through the critical period of late summer and autumn. The evergreen habit permits it to make use of the spring period, when growth conditions average best—a time when an ordinary summer-green plant would be putting all its energies into the building of a new photosynthetic apparatus—as well as the rather frequent periods during the winter months when the temperature is high enough for effective photosynthesis. This explanation has been advanced by Guttenberg (36) for the broad sclerophylls of the Mediterranean region, and by Schimper (80) for the type in general. It seems entirely adequate for the Californian species. It might be added, however, that possibly in *Æsculus californica* we have a still more effective and economical way—the quick production of thin, deciduous leaves for use during the favorable period and their gradual elimination as unfavorable moisture conditions render them dangerous rather than useful.

In figure 17 I have combined the principal factors of the broad-sclerophyll habitat in a way that gives a vivid impression of the whole—rainy and dry season, decreasing summer water-content, with increasing temperatures and evaporation.

THE HABITATS OF THE TWO CLIMAXES CONTRASTED.

The topic that naturally follows is comparison of the respective habitats of the two broad-sclerophyll climaxes, forest and chaparral. Both communities are typically represented on Jasper Ridge, occupying opposite sides of the same ravines, and two subcommunities of the chaparral as well. Care must be exercised in extending the conclusions here drawn to the two climaxes in general, for it is of course true that the factor values noted upon the slopes of a single hill do not in detail perfectly represent the averages that characterize great regions. It may be said, moreover, that given freedom from disturbing agencies, the more xerophytic community, through the reactive influence of the vegetation, might continue its mesotropic development until forest replaced chaparral. Certain determination of this point in any single given case is very difficult. Detailed examination of the tension areas at Jasper Ridge failed to produce satisfactory evidence, either positive or negative. For the present purpose, the question may be settled with sufficient certainty by treatment in line with the discussion upon page 74.

Theoretically, there must be a region intermediate between those clearly dominated by forest and by chaparral where the control is in suspense, and here any decided local variation in habitat toward xerophytism or mesophytism, as would result from opposite hill or ravine slopes, would bring about permanent control of a limited area by one or the other climax. All the evidence points toward the southern Coast Ranges as a region of this nature, and it therefore seems safe to make use of the data obtained at Jasper Ridge in illustrating the differences between the larger units. Further, the differences here are likely to be close to the minimum in degree which are able to bring about the differentiation of climaxes, and are of special interest on that account. Such a comparative evaluation must of necessity include the reactional effects of vegetation upon habitat, accumulated through a long period of development. This is as it should be, since in the interplay of primary and reactive factors we find the "continuing causes" of the vegetation.

Summarizing and commenting upon the differences between forest and chaparral habitats, we attain the following results:

As to soil, humus in the chaparral is very scanty, but in the forest is abundant—nearly 2 per cent by weight in the surface layer and considerable to the depth of 1 meter. In water-content there is large difference during the rainy season, the forest having the greater amount. At this time the surface layers are most important, since the major part of the absorbing roots is contained therein. It is here, too, that the water-content differences mainly show themselves, being practically negligible at the depth of 1 meter. As the dry season advances, water-content values in both communities and at all depths converge, and at its culmination they are all very close together, and the correspondence is rendered still more striking by comparison with the wilting coefficient in each case. In brief, there is notable difference in the actual amount of water available, but at the critical period conditions are about equally severe in both communities. In water-retaining capacity the only noteworthy feature is the relatively high value in the surface soil of the forest community, due to humus. As to soil temperature, the comparative march is the reverse of water-content; the values are closely similar in the wet season, but widely divergent in the dry, the chaparral being much the higher.

As to atmospheric factors, we may dismiss rainfall, cloud, fog, and wind as immaterial to the present local problem. The light impinging upon a leaf of the foliage canopy is much greater in chaparral than in forest, because of the fewer obstacles to its transmission and the reflection and diffusion from the light-colored soil-surface. The intensity in the shade is considerably less beneath the forest canopy, both absolutely and proportionally. The fact that the shade intensity beneath *Arctostaphylos* is practically the same as in the forest indicates that the leaf character is determinative—the sparse needle foliage *vs.* the broad leaves of the other shrubs and the trees. Temperature and relative humidity data are unsatisfactory, but their effects relative to the present purpose are largely included in evaporation. The differences in this factor, though not strikingly great, are constant throughout the year, the *Adenostoma* chaparral being the highest and the *Arctostaphylos* chaparral intermediate. This conclusion is drawn from the values obtained at the top of the vegetation. The rate at the surface of the ground does not show differences of import to the problem in hand.

It may be objected that the evaporation values used here are affected to an unknown degree by the presence of abundant vegetation. In order to discover something of the actual comparative

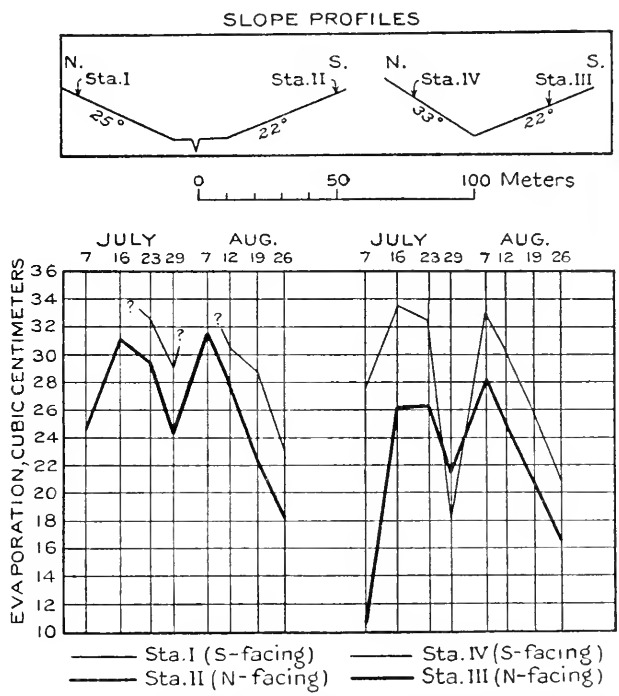


FIG. 18.—Evaporation during the dry season of 1915 on opposite north- and south-facing bare slopes. Foothills of the Santa Cruz Mountains, near Palo Alto.

values upon opposing north and south slopes, uncomplicated by reaction, a short study was made in the hills near Stanford University in the summer of 1915, an account of which is inserted here. Evaporation was measured upon the contrasting north- and south-facing slopes of two ravines, distant about 5 km. from Jasper Ridge. The profiles of these are shown in figure 18. Stations 1 and 2 were 15 meters, and stations 3 and 4 were 18 and 15 meters, respectively, above the valley floors. The slopes were bare of shrubs and trees, the vegetation being largely wild oats, which, with the other herbaceous plants, were dead and brown at the time of the study. The stalks were cleared from the vicinity of the instruments and the effects of vegetation were thus eliminated. The atmometers were installed July 1, and were visited at approximately weekly intervals until August 26. Unfortunately, three readings at station 1 were lost through interference by cattle, which did not respect the chicken-wire defenses. Except for one reading in stations 3 and 4, the south-facing slopes show the higher evaporation-rate. The reversal on July 29 is hard to understand, but may possibly be due to experimental error. Omitting the figures in station 2, which have no corresponding south-facing slope values, we find the following average evaporation-rates:

For the first pair, south-facing : north-facing : : 100 : 85.
For the second pair, south-facing : north-facing : : 100 : 79.
For the 13 complete readings afforded by the two, south-facing : north-facing : : 100:82

There is, then, a distinct difference in evaporation-rate between opposing north and south slopes, when uncomplicated by vegetation. In these open ravines with comparatively gentle slopes the average rates were as 4 to 5. If they had been as steep-sided as certain ravines at Jasper Ridge, the contrast would doubtless have been greater.

We have here sufficient data to explain the greater size and luxuriance of the plants growing upon the north-facing slopes, and the absence of the more mesophytic species from the south-facing exposures. Many factors are indirectly involved, but fundamentally the problem is one of water-balance. During the height of the rainy season there is in both habitats an abundance of soil-moisture and a minimum of evaporation. But the air and soil temperatures are low, and there is consequently little growth. As the temperature rises, the rate of growth increases accordingly, but at the same time the rains are diminishing in frequency and amount, finally ceasing entirely, and the evaporation-rate is going up. It has already been stated that the period when most of the growth occurs is in the spring months, culminating in April. The amount of actual growth during this time, other things being equal, will depend upon the ratio of water-supply to water-loss, and plainly this water-balance is more favorable upon the north-facing slope inhabited by forest. The size of the full-grown plant of a given species depends largely upon the turgor of the growing cells, and a healthy condition of turgor is conditioned upon a water-supply that will more than compensate for the loss by evaporation. If the supply is so scant or the loss so severe that the water-balance is barely maintained at equality, the plant and its organs will be small. If either member of the system varies in such a way that the supply is well in excess of the loss, rapid growth will result. The ever useful example of the stump sprout illustrates this point. The water-supply which formerly fed a full-sized shrub is concentrated upon a few small shoots, which grow for a time with surprising rapidity (see p. 86), although no decrease has occurred in the rate of loss. The size and luxuriance of the plants are therefore greater upon north-facing slopes, where soil-moisture is more abundant and evaporation less rapid during the growing-period.

To account for the absence of the more mesophytic species from the south-facing slopes, we must appeal to the dry season. It has been shown that the soil-moisture contents of the two slopes, considered in relation to the wilting coefficient, are about equally unfavorable during the critical period. This is not true, however, of the evaporation-rate, which is considerably higher in the chaparral community. A seedling of a mesophytic forest species, which might conceivably obtain a start during the spring months, though not making much increase in size, in the chaparral habitat, would be very likely to succumb during the ensuing critical period, when the high evaporation-rate had made the water-balance still less favorable.

Since the plants of the forest, because of their size and abundance, use more water than the chaparral species as food material and lose more through their enormously great expanse of foliage, more is withdrawn by them from the soil. The much more rapid depletion of the water-content during the spring months, resulting from this, is perfectly evident in figure 8. Thus the very luxuriance of the forest vegetation is itself the prime cause of the reduction of water-content practically to the low level of the chaparral.

Our conclusion, then, extended to the larger vegetation units, is that the fundamental distinguishing difference between the two broad-sclerophyll climaxes—their continuing cause, so to speak—is in the water-balance and its variations, whatever the indirect factors influencing it; that its importance is equally divided between wet and dry seasons, the greater excess of supply over loss in the forest during the growing-season explaining the size and luxuriance of the plants living there, and the higher evaporation-rate in the chaparral during the dry season, with equally severe soil-moisture conditions, accounting for the absence of mesophytic species in that habitat.

V. DEVELOPMENT.

THE CLIMAX REGIONS OF CALIFORNIA.

In a region of slight relief and uniform climate, such as the Mississippi Basin or the Great Plains, a single climax extends for hundreds or even thousands of miles. In California the case is very different. The extremes of latitude and altitude, the proximity of the ocean, and the barrier influence of high mountains upon moisture-bearing winds all operate to bring about great and abrupt climatic differences, and therefore great vegetational complexity. Instead of a single climax community there are a half dozen, each, though limited in area, comparable to such a community as the Great Plains grassland or the eastern deciduous forest. Successional investigation has not proceeded far enough to enable us to define these climaxes with accuracy. The following outline is tentative, and is given merely that we may properly place the communities with which we are dealing.

The conifer-forest climaxes are three in number, and the first two have important contact relations with the broad-sclerophyll communities. The *Pacific Conifer Climax Formation*, which includes the forests of the coastal region from California to Alaska, is represented in northwestern California by two associations: (1) The *Sequoia sempervirens* association ranges from the northern boundary of the State, in the immediate vicinity of the coast, southward to San Luis Obispo County. South of San Francisco Bay its continuity is much broken. (2) The *Pseudotsuga* association, which has its center in the Puget Sound region, is poorly represented in California, occurring in the interior of the north Coast Ranges. It is confused with other communities, especially the broad-sclerophyll forest, so that the portion included within the State should probably be considered as transitional.

The *Montane Conifer Climax Formation* covers the middle altitudes of the interior mountain region of western America, and the character tree everywhere is *Pinus ponderosa*. In California it is represented by the *Pinus ponderosa-lambertiana* association, which occurs in the middle altitudes of the west slope of the Sierras and on the higher Coast Ranges and the mountains of southern California.

The *Subalpine Conifer Climax Formation* is practically coextensive with the preceding in general range, but lies above it altitudinally. I will not apply a designation to the California subdivision, as it is rather complex, and no successional work has been done within it. It occurs in the higher Sierras and there are isolated outliers elsewhere. The character trees are *Abies magnifica* and *Pinus monticola* in the lower part, and *Pinus albicaulis* and *Tsuga mertensiana* near timberline.

The broad-sclerophyll climaxes, including the broad-sclerophyll forest and the climax chaparral, will shortly be treated in detail. The alpine meadow climax belongs to the highest summits of the Sierras. The desert climax occurs east of the Sierras and the mountains of southern California. The basin sagebrush climax enters the eastern part of the State to some extent, and the coastal sagebrush is locally important in the interior valleys of the south. It is possible that the Great Valley or a part of it is climax grassland. The coastal sagebrush and the grassland are in extended contact with the climax chaparral.

THE BROAD-SCLEROPHYLL CLIMAX FOREST.

Discussion of the climax nature of the broad-sclerophyll forest involves considerable difficulty. Its distribution is patchy, i. e., no extensive area is completely dominated by it. In parts of the region elements of other vegetation types are mingled with it, giving the appearance of a transitional type. Its natural distribution has plainly been restricted somewhat, especially by fire.

The range of the broad-sclerophyll forest is practically coextensive with that of the climax chaparral, and over most of the region there is sharp alternation between the two. The forest is least important southward. In the Cuyamaca Mountains the chaparral covers all slopes of the lower altitudes, the forest being confined to the steepest ravines and similar situations where the moisture conditions are unusually favorable. As we go northward, or upward in the mountains, we find the forest increasing in importance. In the central Coast Ranges it is the regular covering of the steeper north-facing slopes, the chaparral being confined to south slopes and summits. In the San Francisco Bay region the two are roughly equal in importance, and still farther northward the forest continues to gain. Here, however, a new complication arises. *Pseudotsuga mucronata* is present in the most mesophytic situations and rapidly increases in importance northward. In some places it forms pure growth, but oftener occurs in mixture with the broad-sclerophyll trees, the chaparral still holding the south slopes, but steadily decreasing in importance. Finally, we encounter a clear dominance of *Pseudotsuga*, with the broad-sclerophyll trees forming an understory. Ascending one of the southern mountain ranges, we meet with a similar transition, the broad-sclerophyll forest gaining over the chaparral and finally merging with a forest of *Pseudotsuga*, the species of the last being different (*P. macrocarpa*), but to a degree ecologically equivalent to the northern one. In short, the broad-sclerophyll forest is plainly unable to control in the south; it increases in relative importance northward and upward, but just as it begins to show decided signs of dominance over the chaparral, it comes into competition with a coniferous element, to which it soon becomes subsidiary.

Before proceeding to interpretation, certain definitions are necessary. The *climax* is here considered to be the most mesophytic community which a region as a whole, under present climatic conditions, is able to support. Regions nearby have different climaxes, more mesophytic or less so, according to whether the climates are more or less humid, and the climax of the first region might be succeeded by one or another of these, should the climate change in the appropriate direction. The neighboring climaxes are thus *potential climaxes* for the region under discussion (Clements, 21, p. 108). A potential climax is a *postclimax* if it is more mesophytic than the existing one, and a *preclimax* if less so (l. c., p. 109). Frequently a potential climax is actually present in a region, in situations of unusually favorable or unfavorable moisture conditions. An excellent example of a postclimax is the forest which follows the river valleys far westward into the Great Plains region.

In the light of these definitions it is evident that the broad-sclerophyll forest is postclimax in Southern California. The chaparral is plainly in control, although it is certain that its dominance has been extended somewhat by fire. In central California, where the two are rather evenly balanced, the question is difficult, but the tendency of the forest northward to increase its dominance is plain. In such a transitional region, where the actual control is uncertain, the spatial relations of the competing communities depend upon the nature of the topography. In a level country the change is usually seen in a gradual mingling of the species of the two impinging regions. In a broken country, where steep slopes with various exposures are the rule, the situation is otherwise. The differences in atmospheric factors resulting from contrasting slope exposures are in such a region no greater than elsewhere; but because there is here a zone in which the general conditions permit both groups of species to flourish, the relatively slight differentiation of habitat due to the factor of slope exposure exerts a maximum apparent effect upon the vegetation, a sifting of the species into two groups. We therefore find the two communities sharply set off from one another, each in permanent control of its area, with no successional relations between them. Each is the climax within its own little sphere of influence. Such is the relation of broad-sclerophyll forest and chaparral in the central Coast Ranges, the forest permanently controlling the north slopes, the chaparral the south. Passing into the north Coast Ranges, we would expect to find the broad-sclerophyll forest finally attaining a true climactic status, and there is an undoubted tendency in this direction. The effect is spoiled by the competition of *Pseudotsuga*, the addition of which produces a mixed broad-sclerophyll-conifer community, which is apparently the climax of the region in which it occurs. Farther north, the broad-sclerophyll element loses all claim to dominance, becoming a subordinate part of the conifer forest, and possibly a successional stage in its development.

In way of summary, we may say that although no extensive region is completely dominated by broad-sclerophyll forest, nevertheless it must be considered a climax, since it represents a degree of mesophytism between that of the chaparral and the conifer forest, and because it shows plainly a tendency to gain dominance over the chaparral, attainment of which is hindered only by the competition of a still more mesophytic type.

THE CLIMAX CHAPARRAL.

EVIDENCE OF ITS CLIMAX CHARACTER.

The evidence of the climax nature of that type of chaparral that I have designated as such is presumptive and direct. Under the first head four points may be made.

Dominance.—The very fact that the chaparral is by far the most widespread of all the communities within its range (this being especially true in the region of its center of distribution) in itself creates the presumption that the chaparral is the climax. Bearing in mind that there are cases in which an important and widespread community is not the climax of its region, for instance, the *Pinus murrayana* forest of the central Rockies, whose temporary dominance is due to fire, we can not accept this evidence without confirmation.

Stability.—In most areas the chaparral has obviously been in control for a long period of time—so long that there is no evidence existing of previous vegetation of other type. This is not universal, and in any case is not entirely conclusive.

Occurrence on diverse sites as to soil and topography.—The fact that a community is not restricted to a single topographic situation or soil type, but occurs on many, is good evidence of climax nature. This is true of the chaparral in the region where other evidence indicates its climactic character, i. e., its center of distribution.

Adjustment to climate.—In every region there are many plants which are plainly in adjustment with some very special habitat. Such are aquatic plants, halophytes, and species of rock crevices. All of these occur in the chaparral region. But the species of the chaparral itself possess a constant and much specialized character which is plainly a response to a very particular type of climate. The correspondence in area covered by climate and vegetation type has already been shown. If further evidence be desired, it may be derived from the ecologically equivalent "macchie" of the Mediterranean region and its relation to a climate which is almost identical with that of California. It is difficult to escape the conclusion that a vegetation type which is so perfectly adjusted to the climate of its region must be the ultimate or climax type, in that area at least where it reaches its most perfect development.

The direct evidence for the climax nature of the chaparral is derived from a study of the successions themselves, in which we find that all that have been investigated in a rather widely extended exploration culminate in the establishment of this community, and that over much of the region there is no evidence that any other community is superseding it. Detailed consideration of the successions is reserved for a separate section.

EXTENT OF THE CHAPARRAL AS A TRUE CLIMAX.

Because of widespread disturbance by various agents of destruction, it is impossible to set definite and certain limits to the region of true chaparral dominance. Fire occurring in the transition zone between two formations seriously alters the normal relations due to climatic control. Another source of difficulty lies in the fact that much of the original vegetation of the economically more useful land has been totally destroyed by the invading white man, so that it is necessary to reconstruct the original picture from fragments. Certain areas, however, may be fixed upon as chaparral climax which will not be questioned.

The foothills and low mountains of southern California and certain parts of the valleys and mesas are the most certain, and it is probable that exploration of northern Lower California would add a large extent of country to the range of the chaparral climax. In these places *Adenostoma* is usually the dominant species, or if cultivation has largely destroyed the native vegetation, remnants show it to have been so at a former time. Such is the case in portions of the Los Angeles and San Bernardino Valleys and on the broad mesas east of San Diego. As we ascend the higher mountain ranges of southern California, the evidences of climactic character in the chaparral become less and less convincing. Species which belong to the conifer-forest chaparral appear, and there is more and more alternation with patchy areas of broad-sclerophyll and of conifer forest, in which *Pseudotsuga macrocarpa* is the first to attain importance. In this region there has plainly been an increase of the chaparral areas at the expense of the forest, due to the fact that repeated fires in a transition zone favor the extension of the more xerophytic community. Passing northward in the Coast Ranges, we encounter a similar transition, except that there is practically no admixture of conifer-forest chaparral species until we are well north of San Francisco Bay, and that the alternation is with broad-sclerophyll tree species alone. Here, too, the forest areas show frequent evidence of fire restriction. In the southern Sierras there is a belt along the lower foothills where *Adenostoma* and other chaparral species are of great importance, alternating, however, with much broad-sclerophyll forest. As we go northward, the yellow pine zone, with its accompanying temporary chaparral, approaches more and more closely to the Great Valley, so that roughly from the latitude of Sacramento northward the climax chaparral is excluded from the mountains and foothills proper, such scrub species as occur being of the conifer-forest group. It is an interesting fact that in this stretch of the Sierras *Adenostoma* is almost absent. North of Auburn I have failed to find it in four crossings of the foothills and have been able to discover but one record of its occurrence, noted by Dr. Jepson northeast of Chico.

The relations between chaparral and grassland present certain problems difficult and perhaps impossible of full solution. The fact of the greater extension of the chaparral in the past is certain; the magnitude of that extension is the point of difficulty. The very general statement may be made, subject to qualifications about to be indicated, that in central California the lower mountains are controlled by chaparral and the plains by grasses. The character of the transition zone between the two types is as follows:

The first hills are as a rule entirely grass-covered, though even on these, and occasionally out upon the valley-floor, are patches of chaparral. These show absolutely no correlation with altitude, slope-exposure, or soil-type. Their edges are sharp and the shrubs are uniformly developed throughout. They are obviously remnants. Penetrating farther into the mountain mass, the chaparral patches become more and more numerous, but are still arranged purely in hit-and-miss fashion. Farther still, the chaparral controls the greater area, and the grassland forms the patches, which in summer appear like tan-colored inlays set into the green of the scrub. Finally, the grassland disappears, leaving the chaparral in complete control. In such a journey we do not necessarily encounter continually higher altitudes; we are merely penetrating more and more deeply into a mountain complex in which the ridges may all be of similar height. In short, everywhere near the valleys and plains the hills are grassy, while in the depths of the ranges they are covered with scrub. The larger the extent of the mountain mass the greater is the central area of chaparral. Conversely, a small isolated area of hills, though of considerable altitude, may have none. This arrangement is so nearly universal where chaparral and grassland meet that specific examples are hardly necessary, and yet perhaps a graduated series will be of interest.

The Marysville Buttes in the Sacramento Valley are excellent examples of the isolated hill with practically no brush. The highest summit is 630 meters and the slopes are everywhere covered with the typical annual vegetation of the plains. Even here, however, there are suggestions of the chaparral in the presence in small numbers of *Quercus dumosa*, *Q. wislizeni*, and *Heteromeles arbutifolia* (44).

Mount Diablo is also an isolated mass, but of greater extent and height than the Marysville Buttes. Its lower flanks and the surrounding hills are grassy, with patchwork of scrub, and the upper 300 meters are fairly solid chaparral, in which *Adenostoma* is greatly predominant. In the Mount Hamilton Range we have an extensive complex system made up of ridges of similar height. Penetrating the mass at the point where Coyote Creek debouches into the Santa Clara Valley, we encounter grassy hills, but on the first series, and even on the footslope itself, are patchy remnants of chaparral, mainly *Adenostoma*. North slopes are well forested with broad-sclerophyll trees, and this is entirely natural, since these would resist destruction by fire to a far greater degree than would the chaparral, both by reason of their greater size and the better moisture conditions of their habitat. Grassland is nearly continuous over most of the slopes up to the summit of the first main ridge, where there is a very thin forest of *Pinus ponderosa*, with the same meadow vegetation under the trees. Eastward from here we look into the heart of the mountain system, where numerous ridges are covered with an irregular mosaic of chaparral and grassland. The Santa Lucia Range and the mountains of San Benito County may be cited as examples of the many systems in which one finally penetrates to a central region of solid chaparral.

The most convincing proofs of former control of present-day grassland by chaparral are the frequent remnants that painstaking search brings to light. The sharply limited patches in the midst of other vegetation, in which *Adenostoma* is usually most prominent, have already been described. Experience has shown that even a single mature specimen of this plant is almost certainly a relict and not a fresh arrival, since when its mass control is once thoroughly destroyed it reestablishes itself with the utmost difficulty, probably because of special conditions necessary for successful germination, as yet undiscovered. It is fairly safe, therefore, to assume that wherever mature individuals of *Adenostoma* remain, either isolated or in patches, that that species was formerly dominant. Fence-rows, pieces of rocky or unused ground, ravines, etc., are the sort of places where one looks for such evidence. Using this method, which has in some cases been corroborated by historical testimony, it has been possible to demonstrate that dense chaparral once covered extensive areas which are now grassland or under cultivation. For example, the floor of the Santa Clara Valley southeast of Palo Alto, which is to-day one of the great orchard regions of the State, was less than half a century ago solid chaparral. The bare, grassy hills nearby, with their thin young growth of oaks, were similar. Scattered but full-sized individuals of *Adenostoma* along fences and occasional patches of uncleared ground suggest this, but in the present case we have direct historical evidence of the fact.

Mr. G. F. Beardsley, a retired mining engineer now living in Carmel, California, spent several years of his boyhood in this vicinity, and is able to recall with considerable accuracy the general character of the vegetation at that time. About 1870, according to Mr. Beardsley, the present orchard land between Palo Alto and San Jose was solid chaparral, and patches of the scrub occurred on the floor of the valley between San Jose and Gilroy. A demand arose in San Francisco for the massive woody "roots" of the shrubs for fuel, which made it profitable to clear the chaparral from valley and foothills and ship it to the city. Later the value of the land for fruit and grape culture was discovered, which resulted in the almost complete destruction of the brush. Those cleared areas which are not under cultivation are to-day typical California grassland, sometimes with young oaks scattered through them.

A very interesting and significant bit of relict evidence is the occurrence of a typical area of chaparral well out in the Sacramento Valley. This locality, in Colusa County, between Hershey and Arbuckle, was brought to my attention by Dr. H. M. Hall, of the University of California. Here are several sharply defined patches, typical remnants. One occupies a shallow draw running through a cultivated field; another, in an uncultivated piece of level ground, ends abruptly at a fence. In all, *Adenostoma* is by far the most abundant species; it is of very large size (3 meters) and apparently perfectly content with its home. Other species seen are *Arctostaphylos manzanita*, *A. tomentosa*, *Heteromeles arbutifolia*, and *Rhamnus crocea*. Some scattered trees of *Quercus douglasii* grow where the chaparral has been partially destroyed. These localities are 5 to 8 km. distant from the foothills of the Coast Range.

A few words should be added concerning the trees which occur in scattering growth with the grasses. These are deciduous oaks, especially *Quercus douglasii*, and *Pinus sabiniana*. Typical stands of young *Q. douglasii* have been seen where it is certain that chaparral was formerly in control. In some places remnants of chaparral are mingled with the oaks. The habits of this species, moreover, fit it admirably for such a life. It is an abundant seeder, withstands severe drought, and is one of the least shade-tolerant of the California trees. *Pinus sabiniana* is similar in habitat requirements and frequently occurs in chaparral, especially with *Adenostoma*. It is at least a reasonable supposition that the thin woodlands of *Quercus douglasii* and *Pinus sabiniana* which cover great areas in the Coast Ranges and Sierra foothills, often forming a wide zone between the grassland of the plains and the chaparral of the mountains, are secondary, occupying areas which would support climax chaparral but for agencies of disturbance.

It remains to account for the absence of the chaparral in these areas of grassland, where it is hypothetically the climax. Several agencies have operated to bring this about, some of which have already been suggested. Clearing for firewood has been locally effective; clearing for cultivation much more so. By far the most important cause of destruction has been fire. It has been stated that fire favors the extension of the chaparral at the expense of the forest. It is also true that fire, if it occurs with great frequency, favors grassland at the expense of the chaparral. A single burning of chaparral will result merely in a crop of stump sprouts and greater density than before, but yearly burning will inevitably destroy the brush completely or prevent invasion by it. Cattlemen and sheepmen in the early days, according to unpublished Forest Service reports, were accustomed to fire the brush annually in the foothills to destroy it and thereby improve the grazing conditions. This resulted in a great increase of grassland at the expense of the chaparral. Such recent events, however, are of small importance compared with the effects produced by the aboriginal population. The following quotation from Jepson (47) is of interest in this connection:

> "The herbaceous vegetation [in the Great Valley] in aboriginal days grew with the utmost rankness, so rank as to excite the wonderment of the first whites. . . . . This dense growth was usually burned each year by the native tribes, making a quick hot fire sufficiently destructive to kill seedlings, although doing little injury to established or even quite young trees."

Dr. Jepson writes concerning the sources of his information:

> "The statement made in the Silva re periodical burning rests upon evidence gathered by myself from members of the Nyah, Hupa, Pomo and other tribes; also from verbal relations of early Californians."

It may be added that Merriam estimates the Indian population of California west of the Great Basin at its maximum to have been 250,000. Here we have suggested the cause of destruction of the chaparral, or the prevention of its establishment. It is easy to conceive of the possibility of an occasional area escaping disaster, which would account for the fragments near Hershey and others like it. The reason for the scattering woodland of *Quercus douglasii* and other species is also apparent; an occasional year without burning or a succession of such years would permit the successful germination of young trees, which once established would resist the attacks of fire. The patchy transition between grassland and chaparral is also explained, for fires started in the valleys, where most of the Indian population lived, would spread into the surrounding ranges, in various directions and to varying distances. Certain areas would escape, and these would be larger and more numerous toward the interiors of the mountain systems, where paucity of population would reduce the starting of fires to a minimum. The reasons for the burning I have not been able to discover.

It is certain, therefore, that extensive areas which are now dominated by grasses or thin forest of xerophytic trees were formerly controlled by chaparral or would come to support chaparral if destructive agencies were eliminated; and the principal causes of the destruction of the chaparral or prevention of its establishment have been clearing and repeated fires.

As to the exact extent of former chaparral dominance we can not set limits with any degree of assurance. Some areas are made certain by historical testimony and others almost equally so by relict evidence. We are thus led to admit the extreme probability that the great mass of the Coast Ranges, the foothills of the Sierras, and such minor valleys as the Santa Clara were originally dominated by broad-sclerophylls; that areas now inhabited by grasses or xerophytic trees, occurring as isolated patches surrounded by chaparral or forming a more or less continuous zone upon the foothills bordering the major valleys, are such by reason of clearing or repeated fires. It may be necessary to except from this category the ridges of Coast Range and Sierras that immediately surround the southern end of the San Joaquin Valley, which, with the inclosed plains, are desertlike.

There is a possibility, further, that the northern end of the Great Valley itself may once have been dominated by chaparral. The evidence for this is not absolutely conclusive, but is of sufficient weight to justify presentation. The remnant near Hershey, in the Sacramento Valley, shows that the chaparral species are able to grow to their maximum size and to form a solid cover under typical valley conditions. The practical absence of typical chaparral along the northeastern border of the valley (p. 77)—the only break of importance in the whole circle of surrounding foothills—suggests the probability of a former connection across the valley floor. The climax chaparral has apparently been pinched out between the invading mass of the fire-favored grassland and the relatively resistant barrier of the conifer forest.

So far as available data show, there are no constant efficient climatic differences between the areas dominated to-day by chaparral and the Sacramento Valley. Referring to table 1 (p. 19) we find that 44 stations in the southern Coast Ranges, southern Sierra foothills, and Cuyamaca Mountains, which are the regions most certainly controlled by chaparral, give an average of 21.67 inches of precipitation, while 23 stations in the Sacramento Valley average 21.85 inches. Neither is the seasonal distribution notably different, the proportion of total precipitation occurring in the months May to October being, in the case of the chaparral regions, 11.6 per cent, and in the Sacramento Valley 13.9 per cent. Available temperature data are unsatisfactory, as there are no records of mean summer maxima for the Sacramento Valley.

Clements (22, p. 150) has advanced the theory that the Great Valley of California, "from Bakersfield to Mount Shasta and from the foothills of the Sierra Nevada and Cascade Mountains, through and over much of the Coast Range" was originally grassland of the bunch-grass type, *Stipa* being the most important genus, which has been almost entirely replaced by the introduced annual grasses (*Avena fatua* and *A. barbata*) that are so prominent to-day. He admits the unlikeness of the climate, especially in seasonal distribution of precipitation, to that of other regions of grassland climax, but rightly affirms that the climax plant community is itself the best available indicator of climate. The decision rests, therefore, upon correct identification of the climax community. Clements's evidence of grassland dominance is based upon assumed relicts, and my evidence of chaparral dominance is of the same nature. In an area where individuals and patches of both types occur today, the weight of probability would, in my opinion, favor the chaparral plants as being the survivors of the true regional climax. It has already been stated that most of the species of the climax chaparral, notably *Adenostoma*, reestablish themselves with the utmost difficulty once their mass control has been destroyed, and that therefore thoroughly isolated individuals or patches of such plants are almost certainly relicts of former dominance rather than centers of recent colonization. The same is not true in the case of grasses, even the perennial species which make the grassland climaxes. With these, greater mobility and ease of germination bring about a wide scattering of individuals, and the acceptance of isolated plants or patches as true relicts is therefore rather hazardous.

The acceptance of my conclusions as to former control of certain regions (the main mass of the Coast Ranges with its minor valleys, the foothills of the southern Sierras, and perhaps the northern end of the Sacramento Valley) by chaparral does not necessarily preclude the possibility of climatic grassland over much of the Great Valley.

In southern California the contact between chaparral and coastal sagebrush resembles that between the former and the grassland in the central part of the state. The sagebrush, which is undoubtedly climax in certain portions of the interior valleys, has extended its area of dominance at the expense of the chaparral, because of fire.

In conclusion, then, the climax chaparral has transgressed its normal climatic limits along its mesophytic border through its invasion of the forest, fire being the causative agent; on its xerophytic border it has been pushed back a considerable distance by the grasses and xerophytic forest in the north, and by the coastal sagebrush in the south.

SUCCESSIONS LEADING TO THE CHAPARRAL CLIMAX.

Primary Successions.

The areas where primary succession may be observed are limited, the bulk of the area having reached its final stage or being in process of secondary development. Naturally most of the successions are of the xerarch class. Three distinct lines of development have been observed upon primary areas, corresponding with three common modes of soil formation. These are the successions on rock surfaces, on washes and alluvial fans, and on coastal dunes. In dealing with such an extensive and varied region the treatment can not be complete, and there is here a fruitful field for further study.

Development on rock surfaces.—Though most of the chaparral-covered mountains have a uniform, unbroken mantle of vegetation, there are locally extensive areas where bare rock is being invaded. Such successions are much the same in character wherever they occur. The usual lichens and xerophytic mosses cover the surfaces and their establishment is assisted by the abundant scaling of the rock due to sudden temperature changes. Crevice plants as usual are of supreme importance. Among the herbaceous species, *Pellæa mucronata* and *Selaginella bigelovii* are frequent. The most important pioneers are the chaparral shrubs themselves, the successional stages thus being greatly telescoped. *Adenostoma* is perhaps most important among these. *Yucca whipplei* is common in such places in the southern part of the State. Dead remains of shrubs anchored in the crevices show that permanent establishment may be a matter of many generations. Gradually the rock disintegrates and the chaparral shrubs increase in number. It is not uncommon, however, to find a solid cover of chaparral concealing and growing entirely from the crevices of a rock-layer whose surface is barely at all disintegrated. Thus, through a process long in point of time but comprising few stages, the climax community comes to control the bare rock areas.

Development on alluvial fans and washes.—Because of frequent production of fresh surfaces due to erosion and deposition by periodic torrents, there is excellent opportunity for the study of such successions. Alluvial fans and continuous piedmont slopes occur throughout the State, but they are especially well developed in the Los Angeles and San Bernardino Valleys, bordering the high ranges to the north. The physiographic processes involved in their formation are a complex combination of erosion and deposition. The periodic torrents from the mountain canyons and ravines are continually changing their courses, depositing material now here, now there, cutting into deposits already made, and forming new surfaces through both processes. If the cutting goes deep enough terraces are formed whose surfaces are thereafter free from further direct disturbance.

Certain ancient fans now in process of dissection show all stages in the physiographic cycle. There is a very remarkable example south of San Timoteo Canyon which may be viewed to excellent advantage from Smiley Heights, near Redlands. V-shaped ravines, cut sharply into the original smoothly sloping surface of the fan, represent extreme youth. Wider ravines with graded floors approach maturity, and extensive base-leveled areas with occasional monadnocks have reached old age. With such a series it is an easy matter to correlate vegetational development with physiographic age. Invariably upon the flat surfaces of the terraces and uneroded remnants the vegetation is well-developed chaparral, in which *Adenostoma* is commonly dominant, either solid or represented by relict masses. Chaparral covers the newer base-leveled areas also, except where streams have recently coursed over them. In other words, the stable areas, which have had a chance for a relatively long period of vegetational development, support the chaparral community. Further, the composition of the vegetation of oldest terrace-tops and youngest base-levels is practically identical. Since the terrace-tops, with their vastly greater age, have not advanced beyond the stage reached by the recent base-levels, it is plain that that stage is the climax.

The species that inhabit the unstable eroding slopes and the recently formed washes make a very different assemblage. They are mainly short-lived half-shrubs which germinate readily and are able to exist in the unfavorable conditions which such habitats offer. Clements (22) regards this well-marked community as the westernmost association of the sagebrush formation, because of the importance in it of *Artemisia californica*, and gives it climactic rank. His appellation is here tentatively accepted. The area of coastal sagebrush dominance has not been accurately determined, but roughly it covers the plains and low interior valleys of southern California from the Santa Ana Range to the San Jacinto Mountains. Within the climax chaparral it is successional, occurring in both the primary and secondary series. A number of the species extend northward for varying distances, a few as far as the San Francisco Bay region.

A list of the most important species follows, those particularly characteristic of the southern California group being marked with an asterisk (*):

Eriogonum fasciculatum.*	Ramona stachyoides.	Baccharis pilularis.
Symatium glabrum.	Sphacele calycina.	Encelia farinosa.*
Helianthemum scoparium.	Diplacus glutinosus.	Eriophyllum confertiflorum.
Malacothamnus fasciculatus.*	longiflorus.	Lepidospartum squamatum.*
Ramona clevelandi.*	puniceus.*	Artemisia californica.
nivea.*	Ericameria pinifolia.*	Senecio douglasii.
polystachya.*		

Two or three brief descriptions of individual localities will be of interest. The eroding southwest slope of Smiley Heights, apparently a remnant of an ancient fan, near Redlands, is steep and unstable. The species are *Eriogonum*, *Encelia*, *Ramona stachyoides*, and *Artemisia*. The bluff is much dissected into gullies and ridges which present alternating southeast and northwest slopes, and there is sharp vegetational alternation corresponding with the slope-exposure differences. The first two species occupy the slightly moister northwest slopes in relatively close formation, and the last two make a sparse covering on the opposite hot, dry exposures. The alternation is very conspicuous when viewed from a distance. There are thus degrees of xerophytism among the coastal sagebrush species, giving rise to additional successional stages where delicate differentiation of habitats exists. Remnants indicate that the original vegetation of the level summit of Smiley Heights was *Adenostoma* chaparral.

Three successional stages were revealed by study of the dry washes of Mill and Santa Ana Creeks, at the southern base of the San Bernardino Mountains, and of other similar localities. The plants upon the areas which had most recently been water-swept were *Baccharis viminea*, *Salix argophylla*, *S. lasiolepis*, and *Populus fremontii*, suggesting the inception of a stream-bank community, which can survive only as long as the stream holds its course. The second group, a few individuals of which enter with the first, are the coastal sagebrush species. The pioneer of this stage is the almost leafless composite *Lepidospartum squamatum*. Others gradually arrive, until a typical half-shrub community is established. Most important on these washes are the following:

Syrmatium glabrum.	Ramona stachyoides.	Opuntia covillei.
Eriogonum fasciculatum.	polystachya.	bernardina.
Artemisia californica.	Malacothamnus fasciculatus splendidus.	Yucca mohavensis.
Ericameria pinifolia.		Encelia farinosa.
Senecio douglasii.		

The last is confined to the region from San Bernardino to Elsinore, so far as southern California west of the deserts is concerned, and *Opuntia covillei* is replaced by *O. occidentalis* farther west; otherwise the list is representative of the whole. *Selaginella bigelovii* covers large areas of cobbles and sand with dense growth. The third and final stage comes with the establishment of *Adenostoma*. In the younger areas we find it scattered, with many of the above list mingled with it. On the areas longer undisturbed, as well as on the higher terraces nearby, it forms an almost pure growth. Frequently an uneroded island is seen, surrounded by bare water-swept cobbles. Such an area is likely to possess a remnant of pure *Adenostoma*.

In central California, washes, fans, and terraces are not such striking topographic features, perhaps because the mountain fronts are less abrupt and torrential erosion is therefore less powerful. Still, they do occur, and the same developmental stages and the same *Adenostoma* climax are present, though the successional species are somewhat different.

Development on coastal dunes.—A comprehensive study of the strand vegetation of the Pacific Coast is now in progress. A very brief sketch must here suffice. The pioneers upon beach and dune are mainly strand-succulents, such as *Abronia latifolia*, *A. maritima*, *A. umbellata*, *Mesembryanthemum æquilaterale*, *Convolvulus soldanella*, and *Franseria bipinnatifida*. These are followed by a group of half-shrubs, including *Eriogonum parvifolium*, *Lupinus chamissonis*, *Ericameria ericoides*, and *Eriophyllum stœchadifolium*. In the Monterey region, on an area of very ancient dunes, the succession may be traced farther. *Adenostoma* and *Arctostaphylos pumila* follow the half-shrubs and are themselves succeeded by *Arctostaphylos vestita* and other relatively less xerophytic chaparral species. This community is displaced by a low forest of *Quercus agrifolia*, to which, on the Monterey Peninsula, is added *Pinus radiata*. This is the local climax, more mesophytic in type than in the regions adjacent, probably because of more favorable moisture conditions.

Secondary Successions.

Two classes of secondary successions may be distinguished—those after occasional burning or clearing (where the basal portions of the shrubs are left to sprout) and those after thorough destruction of the original vegetation, either by the grubbing out of the underground parts or by burning at very frequent intervals.

In the first case the succession is a short one, bringing a return practically to the original state in a very few years. The composition of the new chaparral is for a time somewhat different from what it was formerly because of the persistence of some of the plants which came in after the fire. The following outline gives the general features of the development as determined by a quadrat study near Palo Alto and observation elsewhere. Most of the species sprout readily from the stump, and the new shoots grow with astonishing rapidity, even in the driest part of the dry season. Six weeks after the Ojai Valley fire of June 1917, sprouts were found which had attained a height of nearly a meter. The sprouts therefore have a tremendous advantage over any seedlings that may start, especially if the fire occurs early in the dry season, since germination can not take place until the rains begin. With the first rains, seeds which have blown in or lain dormant germinate in enormous number and great variety. Among these are many of the shrub species, which gradually decline in number as the years pass. In a permanent quadrat 5 meters square, near Palo Alto, 562 shrub seedlings appeared during the first rainy season. Seven years later the number of survivors (including some new germinations) was 189. Of the first arrivals, 13 per cent were *Adenostoma* and 62 per cent *Ceanothus cuneatus*, although the original growth was nearly pure *Adenostoma*. The greatest number of herbs appeared during the second rainy season. The 2,841 recognizable individuals comprised 28 species, of which all but half a dozen were annuals. Of this large number, only 13 individuals survived until the following November. There is thus a yearly crop of annuals, smaller each season because of competition with plants of greater stature. The shrub seedlings suffer also in competition with the sprouts, which finally dominate the area. A few of the seedlings survive, however, especially those of *Ceanothus*, and form an important part of the stand for a number of years. Ceanothi of several species, when present in large numbers, seem to be indicators of recent disturbance—in other words, chaparral with a large proportion of *Ceanothus* is likely to be a penultimate stage in a secondary succession.

When the chaparral is utterly destroyed, whatever the cause, the course of development leading to its reestablishment is usually an exceedingly long one. Often a community of a very different stamp takes possession, which, if the disturbing agency frequently repeats its work, may last indefinitely and simulate a true climax. I have already stated my conviction that the grassland of central California is in part a stage in a secondary succession within the region of the chaparral climax, and that certain trees which habitually grow with the grasses, notably *Q. douglasii*, have a rôle in the same process. If such grassland be kept moderately free from grazing and fire, a rough, thick growth of shrubs and half-shrubs often occupies it. These are *Rhus diversiloba, Sphacele calycina, Diplacus glutinosus, Baccharis pilularis;* and they may represent a further stage in the reestablishment of the climax.

In southern California the coastal sagebrush plays an even more important part in the secondary successions than in the primary. Great areas of it cover the mesas and lower foothills, and its spatial relation to the chaparral is usually exactly analogous to that of the grassland of central California. There is the same patchy alternation between the two, with decrease of the half-shrubs and increase of chaparral as one penetrates a mountain mass. No relation to atmospheric, soil, or slope factors can be made out, and the inevitable conclusion is that it has replaced the chaparral because of the destruction of the latter by repeated fires which, starting in the valleys, the centers of human habitation, have spread varying distances into the foothills. Here again we find the chaparral following the forest into the mountains, itself followed by the coastal sagebrush, fire favoring the more xerophytic community in each case. The most important species in the secondary coastal sagebrush are *Eriogonum fasciculatum, Ramona nivea, R. stachyoides,* and *Artemisia californica.* Often they are mixed, but sometimes one encounters great stretches of a single species almost pure. The last two are characteristic secondary species as far north as Monterey Bay. In the valley of the Carmel River I found a deserted vineyard that was thickly grown up to these two species—excellent evidence of their rôle in secondary development.

VI. ECOLOGICAL CHARACTER OF THE BROAD-SCLEROPHYLL SHRUBS AND TREES.

As a text for this chapter I will quote a paragraph from the pioneer of physiological plant geography. He is characterizing the broad-sclerophyll type in general (80, p. 510).

"The trees are usually low, their stems generally massive, and the branches gnarled. The leaves are at most of moderate size, about as large as the leaves of laurel or oleander, usually smaller, or even very small; they are scarcely ever compound, as a rule narrow, lanceolate or linear to acicular; their margins are usually entire. The leaves are not generally placed with their flat surfaces perpendicular to the strongest light, but usually avoid it by assuming an oblique or parallel position. They are either destitute of an air-containing tomentum, or this is confined to their under-surface; on the other hand glandular hairs are not uncommon on both leaf-surfaces. Even when there is no tomentum the leaves comparatively speaking are seldom shiny, but more frequently, even if smooth on the surface, are dull, perhaps owing to exudations of resin, and often bluish. Histologically the foliage is characterized by the thickness of the walls of all the cells, including even the parenchymatous ones, by the abundance of sclerenchyma, by the strong development of cuticle, and by the diminution of the intercellular spaces; these qualities in the aggregate give the leaf its characteristic, stiff, leathery consistency."

In the large, this is an adequate brief characterization of the California broad-sclerophylls. The following detailed analysis will confirm Schimper's statements in the main, at the same time pointing out features in which the California species diverge from his generalizations.

GROWTH FORM.

A very great majority of the California broad-sclerophylls (88 per cent) are shrubs. In Raunkiär's scheme (83) they would be classed as nanophanerophytes. The height of mature individuals is naturally variable. *Adenostoma* may be found, under various conditions, 3 dm. high to 4 meters high. The average for all shrubby species, for the region as a whole, may fairly be placed between 1.5 and 2 meters. In a single locality the height of the individuals of all species is usually remarkably uniform. A few species, which do not usually occur in abundance, habitually rise above their neighbors. Such are *Heteromeles arbutifolia* and *Garrya elliptica* and those which are potential trees. The broad-sclerophyll trees come mainly under Raunkiär's class of mesophanerophytes (8 to 30 meters). *Castanopsis* occasionally attains a greater height, and probably *Pasania* and *Arbutus* also. Most of the trees reach great size under favorable conditions. The diameters of the largest specimens that I have measured are as follows: *Quercus agrifolia*, 2.1 meters; *Quercus chrysolepis*, 1.8 meters; *Arbutus menziesii*, 1.5 meters. Greater diameters have been reported for these species, and Sargent (79) reports 3 meters as the maximum for *Castanopsis*, 1.8 meters for *Pasania*, and 1.5 meters for *Umbellularia*.

The branching of the shrub species is notoriously close and intricate, and the clump habit is almost universal, partly but not wholly due to fire. Many of the tree species show a similar manner of growth—several stems from a single base (often because of fire)—and contorted assurgent or horizontal branches. *Quercus agrifolia* is a notable instance, with its branches of enormous size frequently resting on the ground. Most of the trees are marked by great spread of branches rather than by height. A specimen of *Quercus agrifolia* near Palo Alto shades an area 30 meters in diameter, and this is not an extreme case. The deliquescent mode of branching is the rule. Even when there is a distinct trunk, it is soon lost in the branches. *Pasania* and *Castanopsis* exhibit the closest approach to the excurrent type, maintaining a distinguishable trunk almost throughout. Young specimens of *Umbellularia* show the same form very perfectly, so that one frequently takes them at a distance to be conifers. Large trees of this species are usually branched near the base, but the separate stems maintain the excurrent form.

This seems an appropriate place to mention the small but conspicuous group of species which have more or less spinescent branches. These are *Xylothermia montana*, *Ceanothus cordulatus*, *C. divaricatus*, and *C. incanus*.

ROOT SYSTEM.

Somewhat scanty evidence indicates that the root systems of the chaparral shrubs, when growing in loose soil, are prevailingly of the "dual type" described by Cannon (19). Such root systems are in part deeply penetrating and in part superficial, the latter making up the greater bulk. Cannon states that the sclerophyll *Quercus agrifolia* and the deciduous *Q. douglasii* and *Æsculus californica* are of this type, and suggests that the deeply penetrating roots, which may reach to the neighborhood of the water-table, are formed in youth, while the more numerous superficial roots are developed later.

The root system of a large specimen of *Adenostoma* growing on Jasper Ridge near Palo Alto was carefully excavated and charted (fig. 19). This plant grew in a spot where the soil was pure sand, gradually compacted downward into undecomposed sandstone. It was impossible to trace the roots to a greater depth than a meter, and this was the only locality on the ridge where excavation was feasible at all. The plant grew close to station 10 of the habitat study series. Its root system was decidedly of the dual type. Figure 19 (lower), drawn as if the roots grew all in one plane, exhibits their vertical distribution. It is very common for a large root, at first horizontal, to bend suddenly downward. Several such, lost at a depth of a meter, were 6 to 7 mm. thick at that point. No tap-root or anything approaching it was found, though every seedling possesses a well-developed one. Small branches of 1 mm. or less diameter were given off rather regularly, but at long intervals, all along the main roots. These terminated in groups of mycorhizal rootlets which were embedded in masses of sand-grains held loosely together by hyphæ.

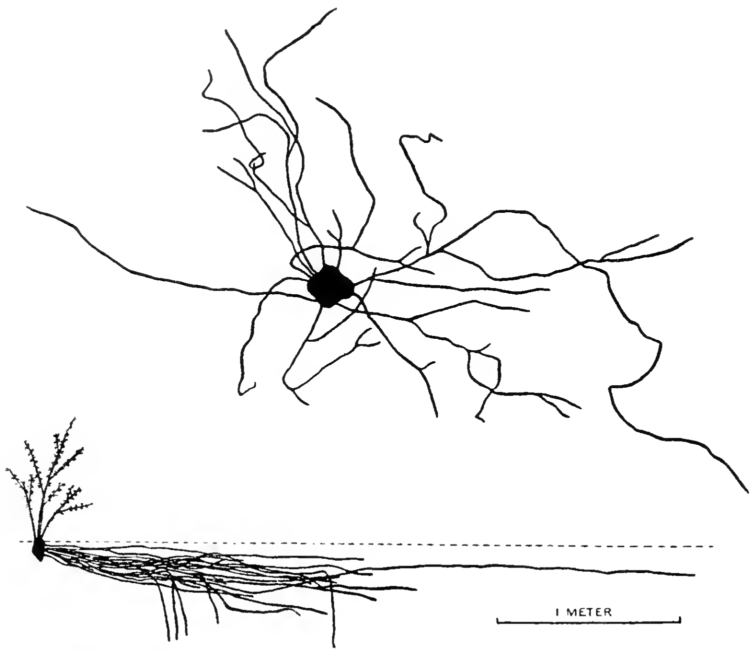


Fig. 19.—Root system of *Adenostoma fasciculatum*: upper drawing shows horizontal, lower shows vertical distribution. In the latter case the roots are arbitrarily drawn as if growing in one plane.

Another excavation of considerable extent was made nearby to learn something of the subterranean relations between the chaparral shrubs and the lower plants that accompany them. The dominants here were *Adenostoma fasciculatum*, *Quercus durata*, and *Arctostaphylos tomentosa*. The individuals grew rather far apart, and therefore the accompanying species were more numerous than usual. A second stratum included *Eriodictyon californicum*, *Rosa californica*, *Helianthemum scoparium*, *Diplacus glutinosus*, and *Syrmatium glabrum*, low shrubs and half-shrubs. A third stratum comprised *Micromeria chamissonis*, *Gymnogramme triangularis*, and a few grasses. Below the surface only two strata were distinguishable. The upper one, about 20 cm. in depth, with some humus, was fairly well filled with the roots from the second and third aerial strata, together with great numbers belonging to the dominants, which were most conspicuous because of their large size. Below 20 cm. were found only the scattered, deeply penetrating roots of the dominants.

General observation shows that the three principal species of Jasper Ridge, *Adenostoma*, *Quercus*, and *Arctostaphylos*, all possess the dual root system. Its usefulness is apparent. During the winter and spring, when most of the year's growth is accomplished, the abundant superficial roots absorb large quantities of water. The humus in this stratum both increases water-retaining capacity and adds to the supply of other food materials. During the dry summer the deeply penetrating roots supply the plant with the minimum amount of water necessary to tide it over the critical period. It is inevitable, when one recalls the extreme desiccation of the surface soils, that the superficial roots cease functioning during the dry season. The dual system is of course apparent only in plants growing in ordinary soil. Where the rock is at the surface, which is very frequently the case, the roots penetrate the crevices wherever they can, without observable system.

Eriodictyon californicum has a very different root plan (fig. 20). The main roots are few, and they travel close to the surface, often from 1 to 6 cm. below it, and occasionally one turns abruptly down-

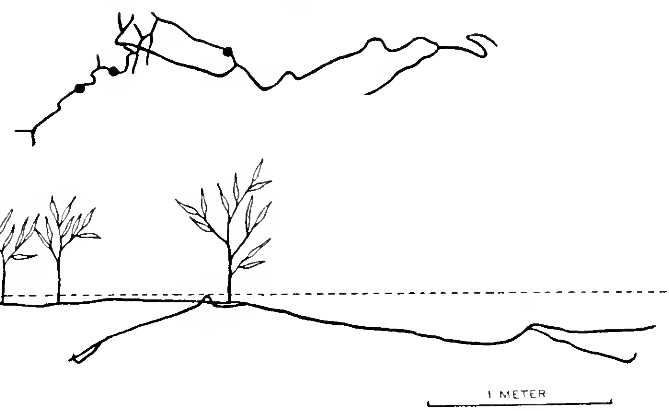


Fig. 20.—Root system of *Eriodictyon californicum*. For explanation, see fig. 19.

ward to the deeper soil-layers. From the horizontal portions sucker shoots appear, so that a number of apparently independent plants are often found to be connected below ground. Whenever the roots are exposed, as by erosion, they produce shoots abundantly. The roots of *Eriodictyon* are useful, therefore, for propagation as well as for absorption.

The three principal chaparral species of Jasper Ridge, *Adenostoma fasciculatum*, *Quercus durata*, and *Arctostaphylos tomentosa*, have been proved to be mycorhizal. In the excavations no normal root-hairs were seen, but it is hardly reasonable that the most deeply penetrating roots should be associated with fungi. The mycorhizas are most abundant naturally in the upper soil layers, where there is most humus. Pockets of nearly pure humus were occasionally found, probably derived from rotted roots, which were thoroughly penetrated by the coralloid rootlets. The mycorhizas were by no means confined to the regions of abundant humus, however. The roots which penetrated the pure sand below the humus layer were almost as well supplied with the fungi. In station 2, where the soil is merely a slightly decomposed clayey sandstone, well-developed mycorhizal roots of *Arctostaphylos* were taken from tight crevices between the fragments.

The best material for study was obtained from *Quercus durata.* The last few centimeters of the roots were found to branch freely, giving off numerous clumps of blunt-tipped coralloid rootlets, each clump firmly embedded in a mass of sand-grains bound together by a network of fungal hyphæ. The hyphæ were of two kinds: (1) very small, transparent, branched, quite certainly non-septate, much more abundant than (2), doing most of the sand-binding; (2) diameter twice or thrice that of (1), branched, very dark brown, some opaque, others only partially so, plainly septate. What appeared to be tight bundles of hyphæ of the septate type were seen, simulating rootlets. A cross-section of a mycorhizal root of this species is given in plate 20A. The dense felt of mycelium completely sheathing the root is well shown, and the hyphæ are seen to penetrate between the cells of the cortex, so that some of the outer ones are apparently isolated from their neighbors. The strands which originally extended out into the soil have, of course, been lost in the process of slide-making.

THE LEAF.

THE DECIDUOUS ELEMENT.

Of the 91 species listed on pages 113 to 120 as being included in the broad-sclerophyll communities as dominants, 18 or 19.8 per cent are deciduous. These are as follows (two or three species which lose their leaves in late winter or spring are classed as evergreens):

Corylus rostrata californica.*	Amelanchier alnifolia.*	Acer macrophyllum.*
Quercus breweri.	Prunus demissa.*	Æsculus californica.
douglasii.	emarginata.*	Ceanothus integerrimus.
garryana.*	subcordata.	parryi.
kelloggii.	Cercis occidentalis.	parvifolius.
lobata.	Acer glabrum.*	sanguineus.*

Omitting those which are not characteristically Californian (marked by asterisk), the number is reduced to 10, or 11 per cent. The relation of the evergreen habit to the Californian habitat is further shown by a comparison of the three communities. The climax chaparral, most characteristically Californian, with a total of 44 dominant species, has no deciduous dominants, the broad-sclerophyll forest, with the small total of 13, has 4 deciduous, or

30.8 per cent, the conifer forest chaparral, with 29 dominants, has 12 deciduous, or 41.4 per cent. Of these 12, 7 are not characteristically Californian, ranging far beyond the boundaries of the State. It is thus evident that the most characteristically Californian community is made up entirely of evergreens, so far as its dominants are concerned, and that the community which has the greatest proportion of deciduous species is also the least characteristically Californian. Further discussion of the leaf will be confined to the evergreen species, or, in other words, to the broad-sclerophylls.

EXTERNAL CHARACTERS.

Compound leaves.—Of the 74 broad-sclerophyll species, only 2 have compound leaves. These are *Berberis pinnata* and *Xylothermia montana*. The leaves of the first are pinnate, with 5 to 9 leaflets, and the second palmate, ordinarily with 3 leaflets. In the measurements to follow, the individual leaflet of these species has been taken as the unit.

Form.—Lobing is still rarer. *Fremontodendron californicum* is the only species, and even in this many of the leaves are unlobed. In shape there is great uniformity. Of the 71 species which are neither compound nor lobed, 54 are of the oval type, ranging from orbicular through elliptic to ovate, the great majority being elliptic. Ten are distinctly obovate, 5 are lanceolate or oblanceolate, and 2 (genus *Adenostoma*) are linear and terete. *Adenostoma fasciculatum*, the most important single species, is not a *broad*-sclerophyll at all, but, as already suggested, this is hardly sufficient ground for discarding for the whole type that very satisfactory appellation.

Size.—It is well known that leaf-size is a fairly trustworthy measure of habitat, especially of the moisture element. Raunkiär has proposed an ecological classification of plants upon the basis of this character, which has been recently brought to our attention in the translation by Fuller and Bakke (31). He has established several size-classes based upon the surface area, the upper limits of which are as follows:

	sq. mm.
1. Leptophyll	25
2. Nanophyll (9 by 25 sq. mm.)	225
3. Microphyll (9^2 by 25 sq. mm.)	2,025
4. Mesophyll (9^3 by 25 sq. mm.)	18,225
5. Macrophyll (9^4 by 25 sq. mm.)	164,025
6. Megaphyll	

Some other delimitation of the classes would have served much better for the broad-sclerophylls of California, since most of the leaves seem to group themselves about the division-lines, but for the sake of comparison with other regions it is better to hold to the system that Raunkiär has established. All the leaves to be classified here come under the first four classes, and it may be helpful to state that a leptophyll, if of the common elliptic form, will be about 9 mm. or less in length, and that the upper length limits of the next three classes, assuming the same leaf-form, will be approximately 27 mm., 81 mm., and 243 mm. The sizes of the leaves were determined by a study of the specimens in the herbarium of the University of Minnesota, which has an excellent representation of the Californian flora. To provide for cases in which a species overlaps two classes, three

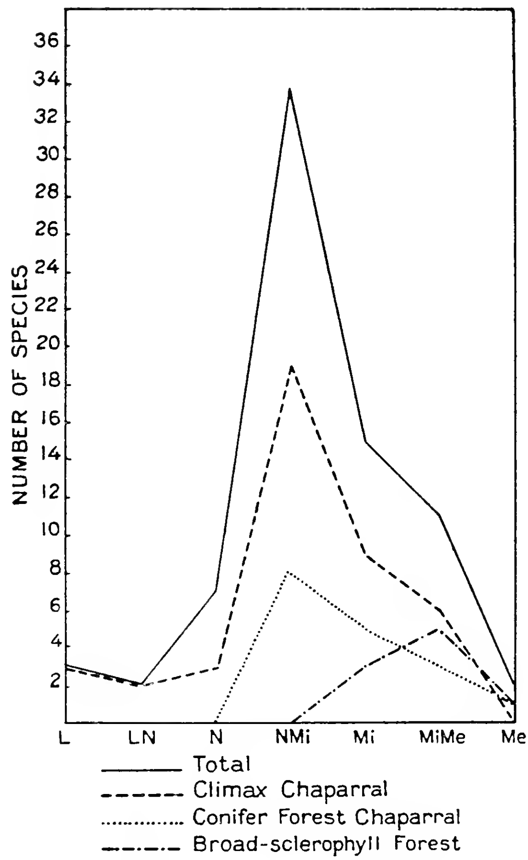


FIG. 21.—Leaf size in the broad-sclerophyll communities. See text.

intermediate categories were made. Because such a large number were found to cluster around the division-lines, it was thought best to include also in the intermediate classes those which were consistently very close to the limit, though not actually crossing it, so far as was shown by the specimens examined.

Figure 21 gives the results of the study. The generally small size of leaf is manifest, all but 11 of the 74 species falling within the three lowest classes—leptophylls, nanophylls, and microphylls. Further-more, there is a very decided maximum in the NMi region, practically half of all being in this class. Species with very small leaves are scarce, though it must not be forgotten that *Adenostoma fasciculatum*, most important of all, is one of these. Considering the vegetation by communities, we find that of 42 important species of the climax chaparral nearly half are of the NMi class, with the rest well distributed on both sides of it. Of 17 species of the conifer forest chaparral, those of class NMi compose nearly one-half, but the others are all of larger classes. Of the 9 broad-sclerophyll forest species, none are smaller than Mi and the maximum lies in the class MiMe. There is thus shown a relation between leaf-size and habitat, the community living in the driest habitat having the largest proportion of small leaves. There is also a correlation between size of leaf and size of plant, since the trees of the broad-sclerophyll forest show consistently greater leaf-size than the shrubs of either of the two chaparral communities.

Attitude.—In the majority of species the leaves lie horizontally, but there is a small group with vertically placed leaves. Certain species of *Arctostaphylos* are prominent here, especially *A. glauca*, *A. hookeri*, and *A. viscida*. In many others there is a more or less prevalent tendency toward the vertical position. *Dendromecon rigidum* has leaves that are ordinarily vertical, but, as in many other cases, they are horizontal in the more mesophytic situations.

Margin.—A majority of the 74 species (58.1 per cent) have entire-margined leaves, although a number of these may show occasional dentation, especially on stump sprouts. 24.3 per cent have leaves that are more or less toothed in the normal fashion; they are serrate, dentate, or crenate. In nearly every case the teeth are shallow. A smaller but conspicuous and characteristic class (17.6 per cent) have notably spiny-toothed leaves that may be aptly described as of the holly type. The resemblance in leaf character between the various species of this group is often striking. This is particularly true of *Prunus ilicifolia* and *Rhamnus crocea*, whose leaves are frequently so similar as to require very minute examination to distinguish them. Eight species (10.8 per cent) have leaves with notably revolute edges. This character appears inconstantly in a number of others.

Pubescence.—Pubescence is not a prominent feature of the broad-sclerophylls. Of the 74 species, 48.7 per cent have more or less pubescent leaves, but in only 17.6 per cent are they pubescent on both surfaces, and often the covering is sparse. The leaves with hair-filled cavities are not considered here unless the hairiness is evident to superficial examination.

Miscellaneous.—Two species, *Eriodictyon californicum* and *Ceanothus velutinus*, have leaves that are varnished and glutinous on the upper surface. In both they are pubescent below. A few species of *Ceanothus* and *Arctostaphylos* have more or less sticky-glandular leaves. Three species commend themselves to the sense of smell—*Myrica californica*, *Umbellularia californica*, and *Eriodictyon californicum*. The last two are widespread and common, and thus give the broad-sclerophyll vegetation a reputation for odoriferousness which it hardly deserves.

The external characteristics of the 74 species are presented in detail in table 12.

TABLE 12.—*External leaf character.*

Compound (2.7 p. ct.):
- Berberis pinnata.
- Xylothermia montana.

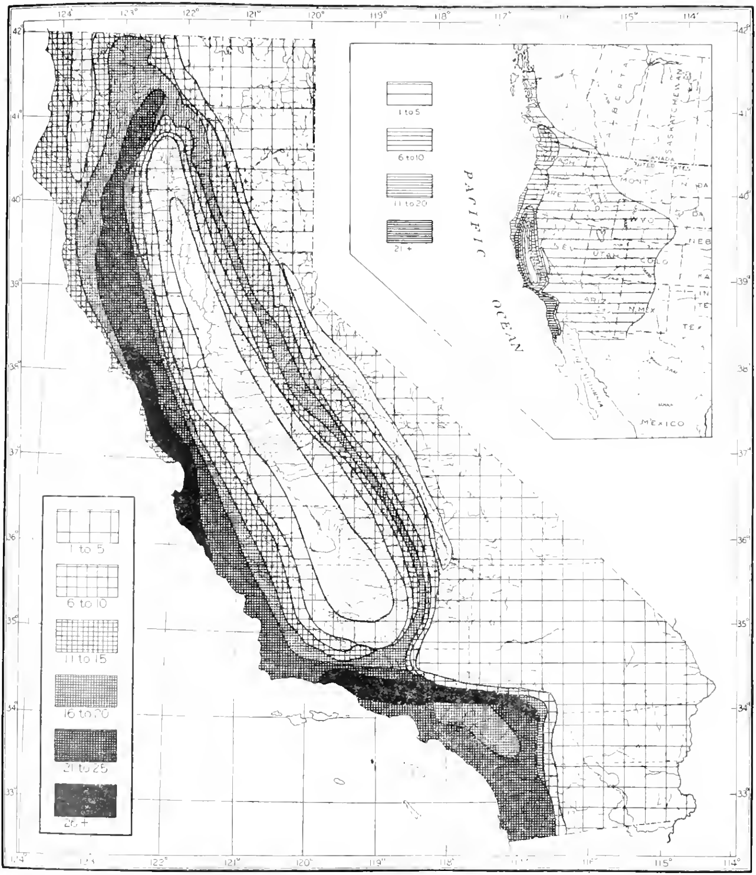
Lobed (1.4 p. ct.):
- Fremontodendron californicum.

Size:
- Leptophylls (4.1 p. ct.):
  - Adenostoma fasciculatum.
  - A. sparsifolium.
  - Ceanothus dentatus.
- Nano-leptophylls (2.7 p. ct.):
  - Ceanothus foliosus.
  - C. rigidus.
- Nanophylls (9.5 p. ct.):
  - Cneoridium dumosum.
  - Ceanothus cuneatus.
  - C. pinetorum.
  - C. prostratus.
  - C. verrucosus.
  - Arctostaphylos myrtifolia.
  - A. nummularia.
- Nano-microphylls (45.9 p. ct.):
  - Quercus dumosa.
  - Q. durata.
  - Q. vaccinifolia.
  - Cercocarpus betulæfolius.
  - C. ledifolius.
  - Xylothermia montana.
  - Rhamnus crocea.
  - Ceanothus cordulatus.
  - C. crassifolius.
  - C. divaricatus.
  - C. diversifolius.
  - C. hirsutus.
  - C. incanus.
  - C. megacarpus.
  - C. papillosus.
  - C. sorediatus.
  - C. spinosus.
  - C. thyrsiflorus.
  - C. tomentosus.
  - Arctostaphylos drupacea.
  - A. glauca.
  - A. hookeri.
  - A. manzanita.
  - A. mariposa.
  - A. montana.

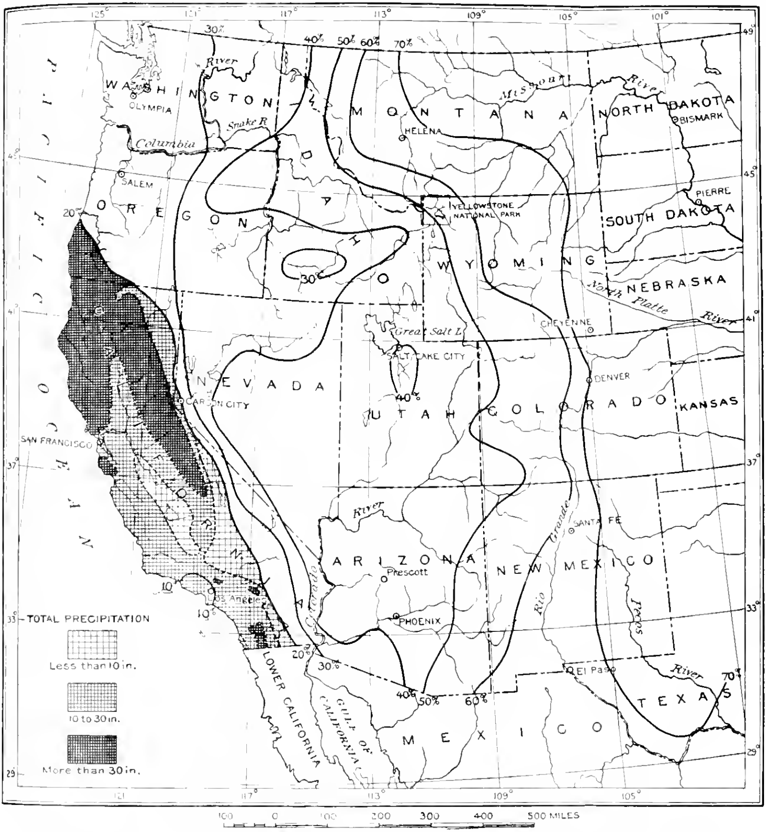
Size—Cont'd.
- Nano-microphylls (45.9 p. ct.) Cont'd.
  - A. nevadensis.
  - A. parryana.
  - A. patula.
  - A. pumila.
  - A. pungens.
  - A. stanfordiana.
  - A. tomentosa.
  - A. vestita.
  - A. viscida.
- Microphylls (20.3 p. ct.):
  - Castanopsis sempervirens.
  - Quercus chrysolepis.
  - Q. engelmanni.
  - Q. wislizeni.
  - Berberis pinnata.
  - Dendromecon rigidum.
  - Prunus ilicifolia.
  - Rhamnus californica.
  - Ceanothus palmeri.
  - Fremontodendron californicum.
  - Garrya elliptica.
  - G. fremontii.
  - Comarostaphylis diversifolia.
  - Xylococcus bicolor.
  - Arctostaphylos andersonii.
- Micro-mesophylls (14.9 p. ct.)
  - Myrica californica.
  - Castanopsis chrysophylla.
  - Quercus agrifolia.
  - Pasania densiflora.
  - Umbellularia californica.
  - Heteromeles arbutifolia.
  - Rhus integrifolia.
  - R. laurina.
  - R. ovata.
  - Ceanothus velutinus.
  - Eriodictyon californicum.
- Mesophylls (2.7 p. ct.):
  - Quercus sadleriana.
  - Arbutus menziesii.

Margin:
- Entire (58.1 p. ct.):
  - Castanopsis chrysophylla.
  - C. sempervirens.

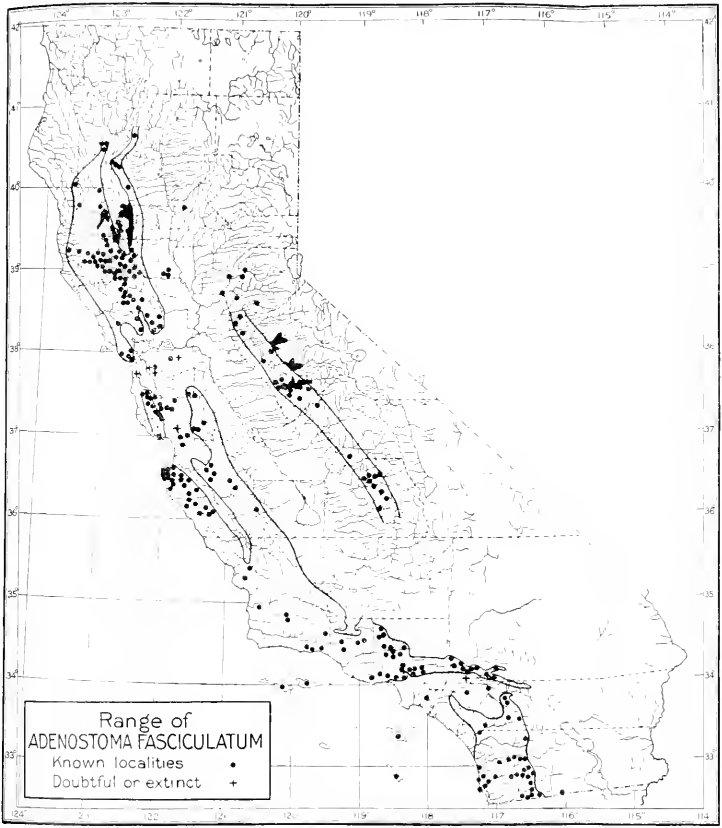
Margin—Cont'd.
- Entire (58.1 p. ct.) Cont'd.
  - Quercus vaccinifolia.
  - Umbellularia californica.
  - Dendromecon rigidum.
  - Cercocarpus ledifolius.
  - Adenostoma fasciculatum.
  - A. sparsifolium.
  - Xylothermia montana.
  - Cneoridium dumosum.
  - Rhus integrifolia.
  - R. laurina.
  - R. ovata.
  - Rhamnus californica.
  - Ceanothus cordulatus.
  - C. cuneatus.
  - C. divaricatus.
  - C. hirsutus.
  - C. incanus.
  - C. megacarpus.
  - C. palmeri.
  - C. spinosus.
  - Garrya elliptica.
  - G. fremontii.
  - Arbutus menziesii.
  - Xylococcus bicolor.
  - Arctostaphylos drupacea.
  - A. glauca.
  - A. hookeri.
  - A. manzanita.
  - A. mariposa.
  - A. montana.
  - A. myrtifolia.
  - A. nevadensis.
  - A. nummularia.
  - A. parryana.
  - A. patula.
  - A. pumila.
  - A. pungens.
  - A. stanfordiana.
  - A. tomentosa.
  - A. vestita.
  - A. viscida.
- Toothed (24.3 p. ct.):
  - Myrica californica.
  - Quercus engelmanni.
  - Q. sadleriana.
  - Pasania densiflora.
  - Cercocarpus betulæfolius.



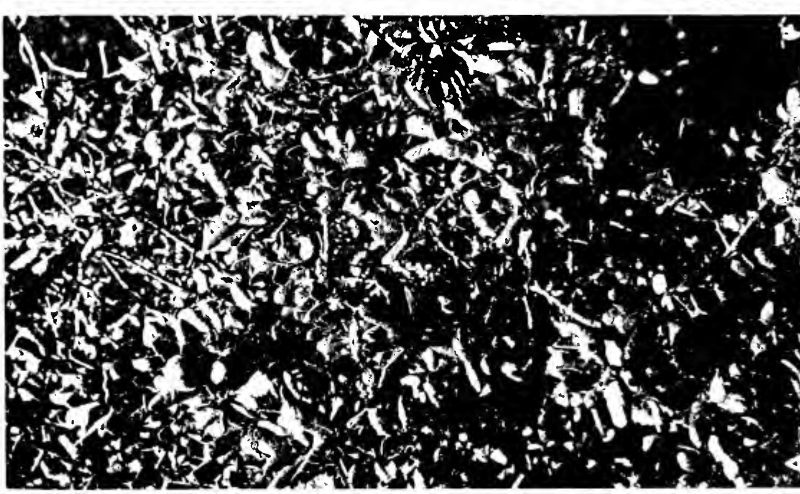
Species-density of broad-sclerophylls, shown by depth of shading, in California and in western North America.



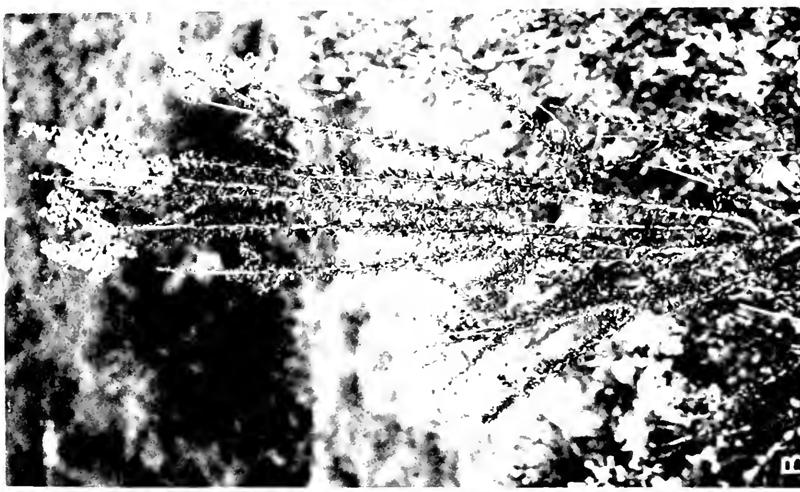
Seasonal distribution of precipitation in western North America, and average total seasonal precipitation in region with less than 20 per cent summer precipitation



Distribution of Adenostoma fasciculatum: dots show authentic localities; solid black, areas where it has been accurately mapped as dominant; crosses show localities which are doubtful or where it probably does not exist at the present time.



A. *Quercus durata.*

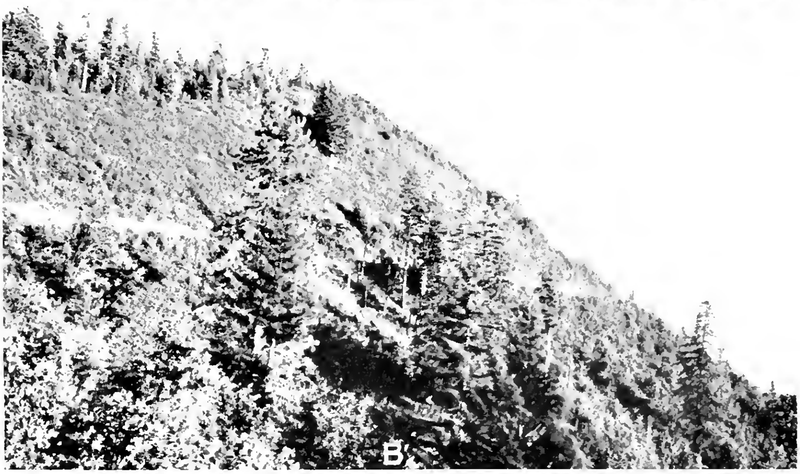


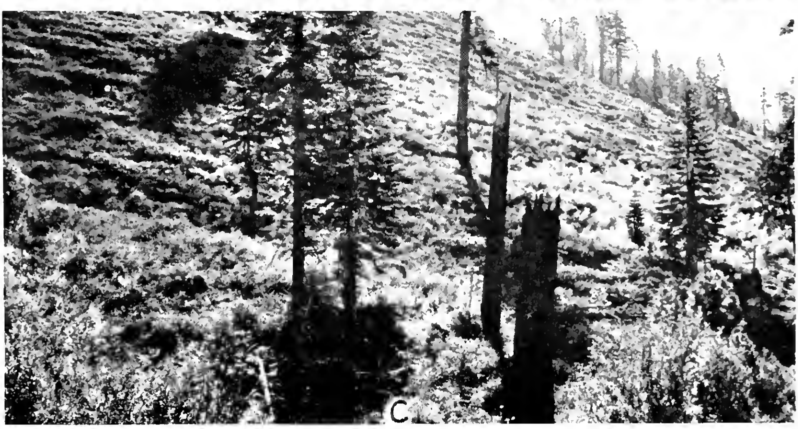
B. *Adenostoma fasciculatum.*

C. *Arbutus menziesii.*

A. *Ceanothus cuneatus.* B. *Ceanothus sorediatus.*

A. *Arctostaphylos glauca*: a large specimen. Mount Hamilton Range, Santa Clara County.
B. *Arctostaphylos viscida*.





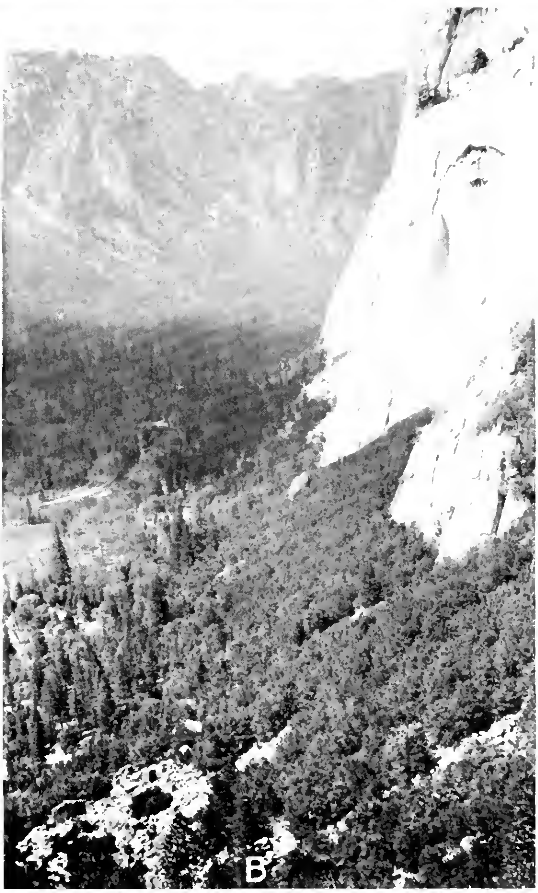
A. Subalpine forest zone in the northern Sierras: conifer-forest chaparral in foreground; Mount Lassen in the distance.

B. Secondary thicket growth of *Quercus kelloggii* and *Q. garryana*, with relicts of *Pinus ponderosa* and *Pseudotsuga mucronata*. South Fork Mountain, Trinity County.

C. Conifer-forest chaparral association: *Arctostaphylos patula*, *A. nevadensis*, *Castanopsis sempervirens*, *Ceanothus velutinus*, *Quercus vaccinifolia*, *Amelanchier alnifolia*; remnants of climax forest. Near Mount Lassen, northern Sierras.

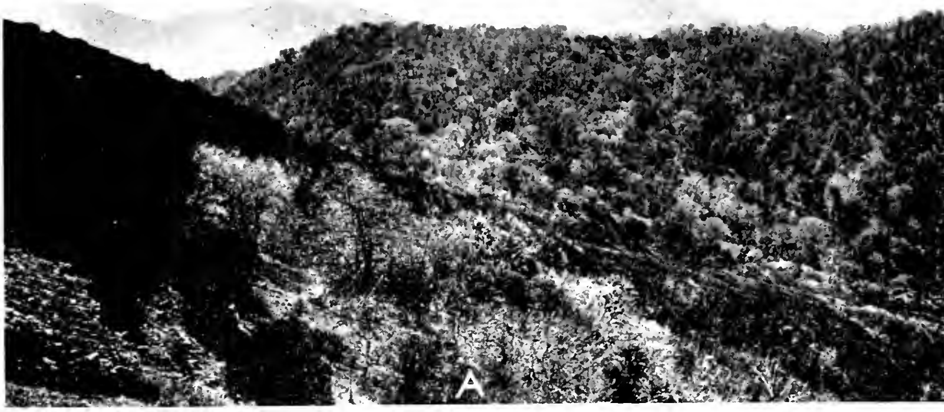
A. Transition between broad-sclerophyll and redwood forests: a group of redwoods on flood-plain in left center; broad-sclerophyll forest (*Pasania-Quercus-Arbutus* association) at right, with admixture of *Pseudotsuga*. South Fork of Eel River, Humboldt County.

B. Undergrowth of *Quercus agrifolia-Arbutus* association: *Symphoricarpos racemosus* most abundant. Near Palo Alto, Santa Clara County.



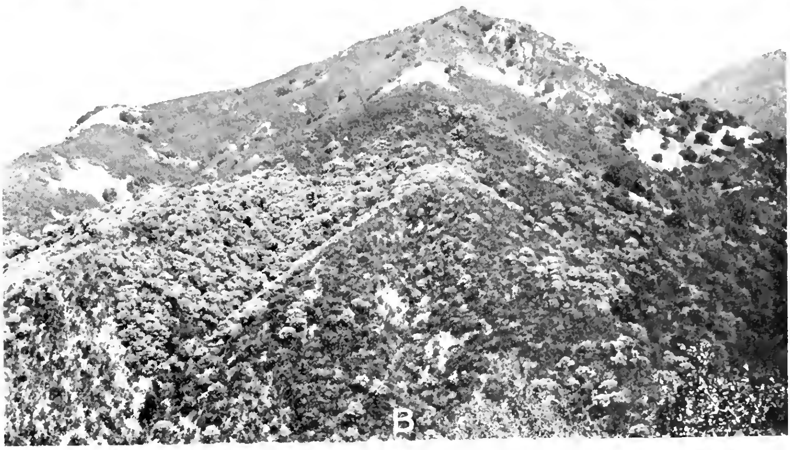
A *Quercus agrifolia-lobata* association on alluvial fan: winter aspect, the *Q. lobata* leafless. Atherton, San Mateo County.

B *Quercus chrysolepis* consociation (successional) on talus. Yosemite Valley.



A. Alternation of chaparral (*Adenostoma* consociation) and broad-sclerophyll forest correlated with south and north-facing slopes. The trees in the immediate foreground are secondary oaks in a grassy area. Santa Lucia Mountains, Monterey County.

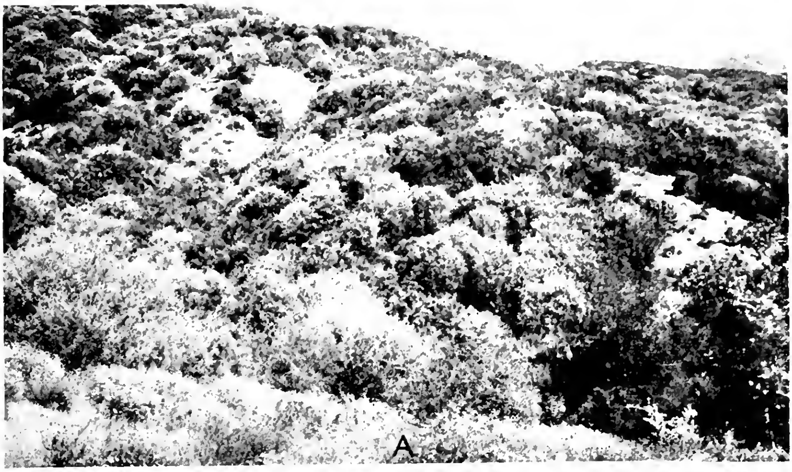
B. Alternation of chaparral (*Adenostoma* consociation) and broad-sclerophyll forest (*Quercus agrifolia-Arbutus* association), corresponding with south and north facing slopes; *Quercus agrifolia*, *Q. kelloggii*, *Arbutus menziesii*, and *Umbellularia californica* (conical form) prominent in the latter; chaparral somewhat disturbed. Chaparral (*Arctostaphylos* dominance) at the top of the north facing slope; also a clearing. Permanente Cañon, east slope of Santa Cruz Mountains, near Black Mountain.



A. Vegetation cover of lower Cuyamaca Mountains: chaparral on all slopes; occasional broad-sclerophyll trees. Viejas Grade, San Diego County.

B. Chaparral cover of Santa Lucia Mountains: *Adenostoma* most abundant; *Arctostaphylos glauca* (light tone) at left; *Quercus agrifolia* in ravine at right; occasional dead stalks of *Yucca whipplei;* secondary grassy areas. Near Tassajara Springs, Monterey County.

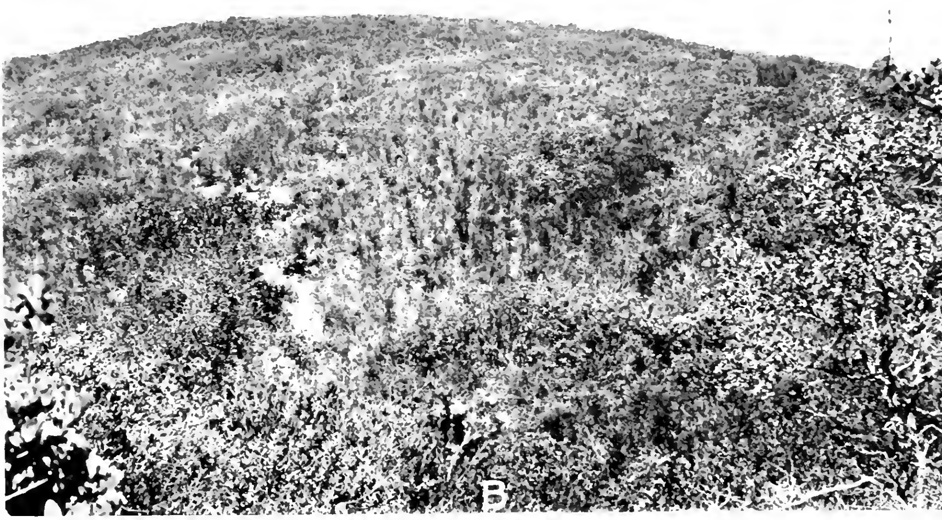
C. Mountains of Ventura County, solidly clothed with chaparral. Near Wheeler Hot Springs.



A. Chaparral of *Adenostoma fasciculatum* and *Ceanothus crassifolius* (light), a common combination in southern California. Near Wheeler Hot Springs, Ventura County.

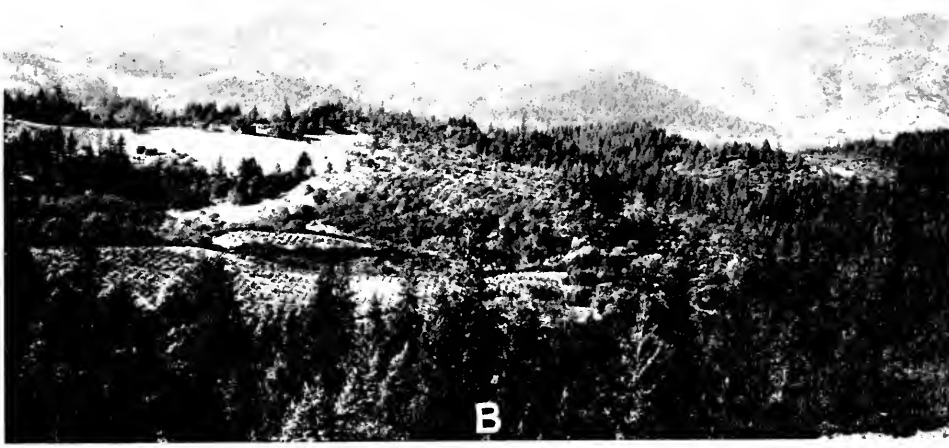
B. Ground cover at Station 3, Jasper Ridge; relatively abundant litter beneath *Arctostaphylos*.

C. Station 2, Jasper Ridge, showing atmometers in position.



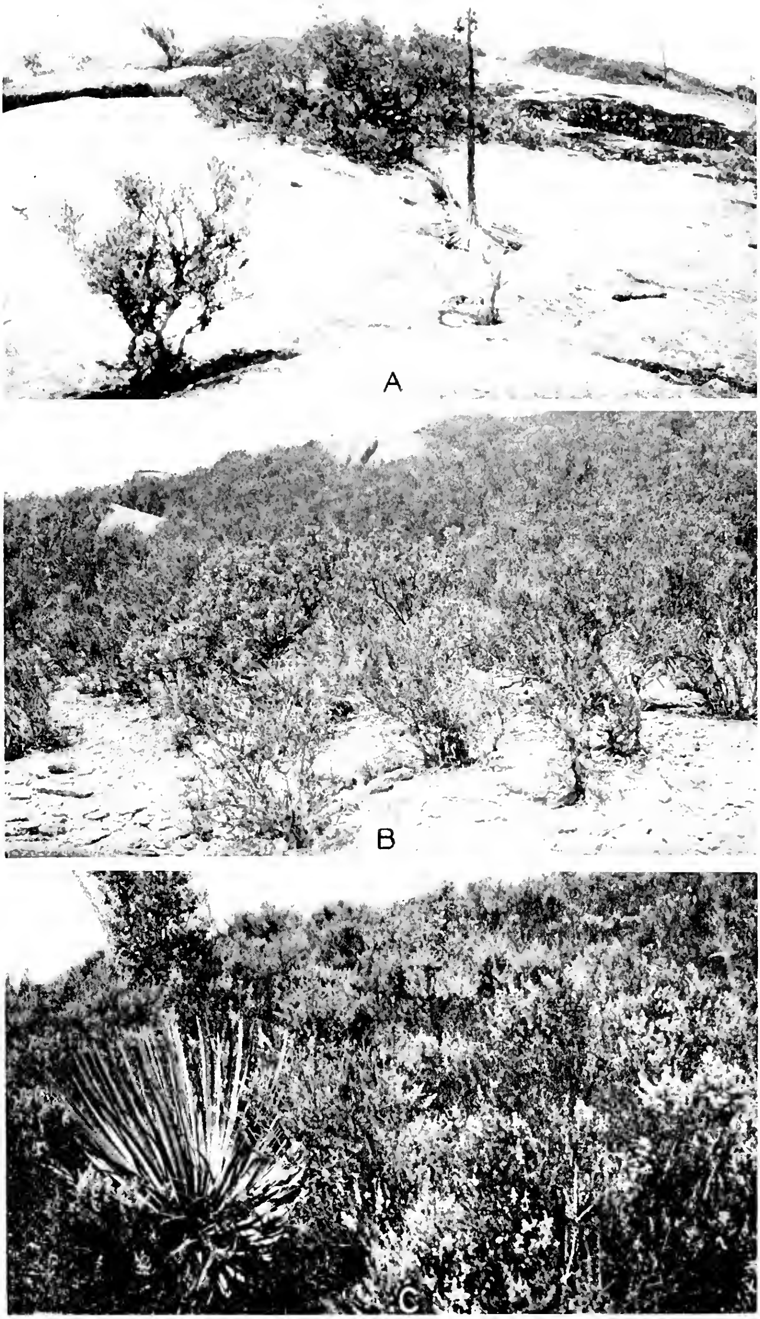
A. Jasper Ridge, vicinity of Station 3 from Station 1; [illegible] and *Quercus durata*.

B. South-facing slope at Jasper Ridge upon which Stations 4 and 5 are located; from vicinity of Station 3.

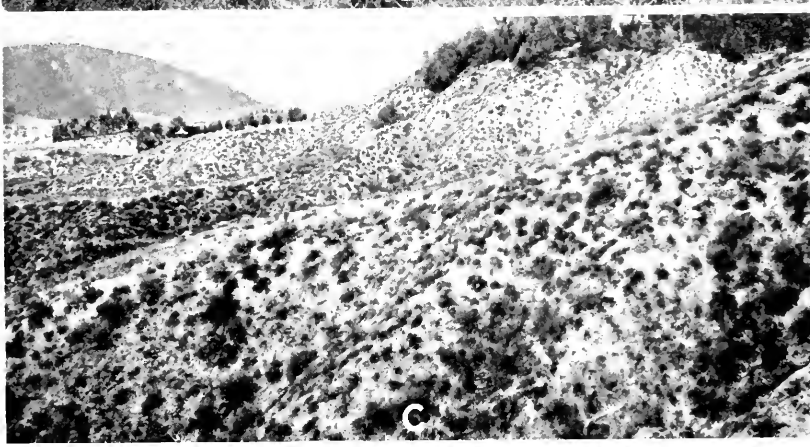


A. *Quercus agrifolia-Arbutus* association on north slope at Jasper Ridge; Stations 7 and 8 are in the area of the picture; chaparral at ridge top.
B. Typical scenery of the interior north Coast Ranges, where the dominating vegetation is a mixture of broad-sclerophylls and conifers, especially *Pseudotsuga mucronata;* secondary grassy areas; Mount St. Helena.

A. Remnant of chaparral (*Adenostoma* consociation) on the floor of the Sacramento Valley, in Colusa County, south of Arbuckle; Coast Range in the distance.
B. *Adenostoma* consociation on east slope of north Coast Ranges; clearing and secondary grassland with *Pinus sabiniana* and *Quercus douglasii* growing with the latter; *Pinus ponderosa* on distant ridges. Beegum, Tehama County.
C. Remnant of original chaparral cover on the slope of an isolated mountain; secondary grassland, with abundant cattle trails; live oaks in ravines. Mount Diablo, Contra Costa County.



A. Primary succession in the climax chaparral region: lichens and mosses on rock surface; *Adenostoma*, *Arctostaphylos*, and *Yucca* as crevice pioneers. Cuyamaca Mountains, San Diego County.
B. Later stage of succession, showing the preeminent importance of the crevices. Same locality as the last.
C. Fully developed chaparral (*Adenostoma* consociation) with *Yucca whipplei*. Same locality as the last.

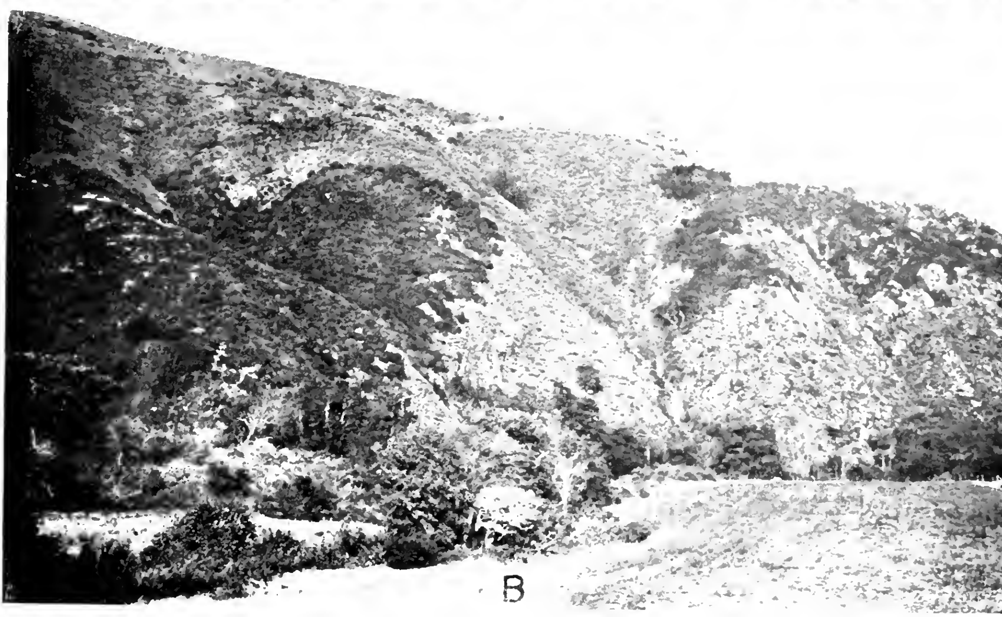


A. Primary succession on alluvial fan: recent wash with scattered pioneers of numerous species; low terrace at right with partially developed *Adenostoma* climax; uneroded remnant at left with *Adenostoma*. Mill Creek Wash, south base of San Bernardino Mountains.

B. Primary succession on alluvial fan: coastal sagebrush on old wash; *Syrmatium glabrum*, *Eriogonum fasciculatum*, and others; *Adenostoma* climax on terrace. Mill Creek Wash, south base of San Bernardino Mountains.

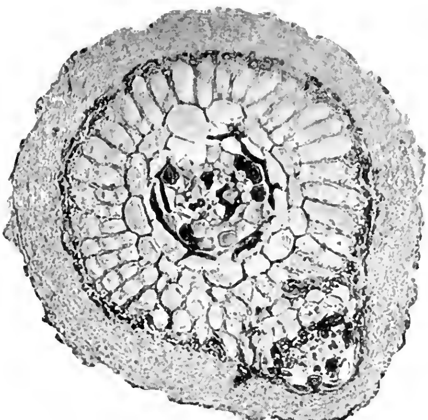
C. Coastal sagebrush on south-facing unstable slope: *Ramona stachyoides*, *Artemisia californica*, *Eriogonum fasciculatum*, *Encelia farinosa*. Smiley Heights, near Redlands.

A. Young stump sprouts of *Adenostoma fasciculatum*.
B. Destruction of chaparral by the Ojai Valley fire of June 1917; underground parts killed in many cases; edge of burned area at top of ridge. Near Wheeler Hot Springs



A. Chaparral-covered mountains north of Arrowhead Springs, San Bernardino Mountains; fire-restricted remnants of *Pseudotsuga macrocarpa*.

B. Relict patches of chaparral *Adenostoma* consociation; secondary grassland on ridge top; secondary coastal sage-brush on slopes too steep for grazing. San Jose Cañon, Monterey County.



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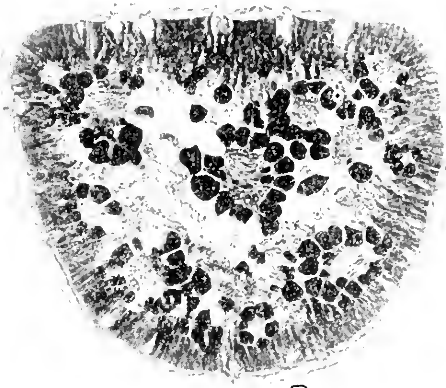

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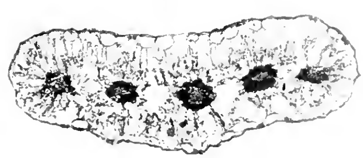


D

A. *Quercus durata:* cross-section of mycorhizal rootlet; note the thick external felt of mycelium, and the hyphæ penetrating between the cells of the cortex. X 170.
B. *Adenostoma fasciculatum:* cross-section of normal leaf. X 75.
C. *Adenostoma fasciculatum:* cross-section of leaf from stump sprout X 70.
D. *Adenostoma fasciculatum:* cross-section of leaf from seedling. X 70.

A. *Adenostoma fasciculatum:* *a* is the normal xerophytic type; *b* is from a shady mesophytic situation (Station 7 at Jasper Ridge).
B. *Adenostoma fasciculatum:* upper row, normal leaves; middle, leaves from a stump sprout; lower, from seedlings.

TABLE 12.—*External leaf character*—Continued.

Margin—Cont'd.
- Toothed—Cont'd.
  - Ceanothus dentatus.
  - C. diversifolius.
  - C. foliosus.
  - C. papillosus.
  - C. sorediatus.
  - C. thyrsiflorus.
  - C. tomentosus.
  - C. velutinus.
  - C. verrucosus.
  - Fremontodendron californicum.
  - Comarostaphylis diversifolia.
  - Arctostaphylos andersonii.
  - Eriodictyon californicum.
- Spiny-toothed (17.6 p. ct.):
  - Quercus agrifolia.
  - Q. chrysolepis.
  - Q. dumosa.
  - Q. durata.
  - Q. wislizeni.
  - Berberis pinnata.
  - Heteromeles arbutifolia.
  - Prunus ilicifolia.
  - Rhamnus crocea.
  - Ceanothus crassifolius.
  - C. pinetorum.
  - C. prostratus.
  - C. rigidus.
- Revolute (10.8 p. ct.):
  - Quercus durata.
  - Cercocarpus ledifolius.
  - Rhamnus californica.
  - Ceanothus crassifolius.
  - C. dentatus.
  - C. papillosus.
  - Garrya elliptica.
  - Xylococcus bicolor.

Surface:
- Glabrous (52.7 p. ct.):
  - Myrica californica.
  - Quercus agrifolia.
  - Q. vaccinifolia.

Surface—Cont'd.
- Glabrous (52.7 p. ct.) Cont'd.
  - Q. wislizeni.
  - Umbellularia californica.
  - Berberis pinnata.
  - Dendromecon rigidum.
  - Heteromeles arbutifolia.
  - Adenostoma fasciculatum.
  - A. sparsifolium.
  - Prunus ilicifolia.
  - Xylothermia montana.
  - Cneoridium dumosum.
  - Rhus integrifolia.
  - R. laurina.
  - R. ovata.
  - Rhamnus crocea.
  - Ceanothus cordulatus.
  - C. divaricatus.
  - C. foliosus.
  - C. palmeri.
  - C. pinetorum.
  - C. prostratus.
  - C. spinosus.
  - C. thyrsiflorus.
  - C. verrucosus.
  - Arbutus menziesii.
  - Arctostaphylos drupacea.
  - A. glauca.
  - A. hookeri.
  - A. manzanita.
  - A. myrtifolia.
  - A. nevadensis.
  - A. nummularia.
  - A. parryana.
  - A. patula.
  - A. pungens.
  - A. stanfordiana.
  - A. viscida.
- Lower surface pubescent (31.1 p. ct.):
  - Castanopsis chrysophylla.

Surface—Cont'd.
- Lower surface pubescent (31.1 p. ct.) Cont'd.
  - C. sempervirens.
  - Quercus chrysolepis.
  - Q. dumosa.
  - Q. engelmanni.
  - Q. sadleriana.
  - Pasania densiflora.
  - Cercocarpus betulæfolius.
  - C. ledifolius.
  - Ceanothus crassifolius.
  - C. cuneatus.
  - C. incanus.
  - C. megacarpus.
  - C. rigidus.
  - C. sorediatus.
  - C. velutinus.
  - Garrya elliptica.
  - G. fremontii.
  - Comarostaphylis diversifolia.
  - Xylococcus bicolor.
  - Arctostaphylos andersonii.
  - A. pumila.
  - Eriodictyon californicum.
- Both surfaces pubescent (16.2 p. ct.):
  - Quercus durata.
  - Rhamnus californica.
  - Ceanothus dentatus.
  - C. diversifolius.
  - C. hirsutus.
  - C. papillosus.
  - C. tomentosus.
  - Fremontodendron californicum.
  - Arctostaphylos mariposa.
  - A. montana.
  - A. tomentosa.
  - A. vestita.

INTERNAL STRUCTURE.

I have examined the leaves of 26 of the representative broad-sclerophyll species of the central Coast Ranges. 7 are trees of the broad-sclerophyll forest and the others are shrubs of the climax chaparral. All the important genera are well represented, and it is reasonable to assume that the selection presented here gives a true picture of Californian broad-sclerophyll structure. The material was collected near Palo Alto and in the Monterey region. It was killed and preserved in formalin-alcohol, cut in celloidin, and stained with safranin and aniline blue. 17 species have been selected for illustration by means of drawings executed by Miss Vinnie A. Pease, of the University of Minnesota. In addition to the general study, measurements were made of thickness of leaf and of upper and lower cuticle in each species (table 13). For the sake of comparison, a group of two sclerophyll species of the redwood-forest undergrowth and one of 5 native deciduous trees have been added. The figures given in the table are averages of 10 measurements, made in nearly

TABLE 13.—*Thickness of leaf and cuticle.*

	Leaf.	Upper cuticle.	Lower cuticle.
Broad-sclerophyll forest:	*microns.*	*microns.*	*microns.*
Myrica californica	80	3.08	1.84
Castanopsis chrysophylla	254	2.63	1.39
Quercus agrifolia	314	3.75	1.80
Q. chrysolepis	219	3.75	2.59
Pasania densiflora	217	2.85	2.06
Umbellularia californica	208	5.58	3.78
Arbutus menziesii	264	2.96	1.80
Climax chaparral:			
Quercus durata	205	2.94	3.21
Berberis pinnata	178	3.82	2.81
Dendromecon rigidum	371	4.20	2.67
Heteromeles arbutifolia	339	11.58	7.57
Adenostoma fasciculatum	562	9.73	9.66
Prunus ilicifolia	345	3.98	2.81
Xylothermia montana	385	5.85	4.68
Rhamnus californica	265	8.25	3.49
R. crocea	246	5.28	2.17
Ceanothus cuneatus	462	4.65	2.96
C. papillosus	214	2.25	1.08
C. rigidus	472	6.86	4.50
C. sorediatus	224	1.12	1.12
Garrya elliptica	365	17.25	9.52
Arctostaphylos hookeri	398	11.82	11.63
A. pumila	362	8.85	5.77
A. tomentosa	355	9.89	11.32
A. vestita	264	12.10	11.44
Eriodictyon californicum	345	1.24	1.05
Redwood-forest undergrowth:			
Gaultheria shallon	432	4.05	2.51
Vaccinium ovatum	365	4.57	1.61
Deciduous species:			
Salix lasiolepis	111	1.35	6.37
Alnus rhombifolia	111	1.12	7.50
Quercus lobata	160	2.06	12.75
Platanus racemosa	149	2.21	12.00
Acer macrophyllum	106	1.16	6.75
Summary:			
1. Broad-sclerophyll forest	222	3.52	2.04
2. Climax chaparral	336	6.36	5.23
3. Average of classes 1 and 2	314	5.69	4.43
4. Redwood-forest undergrowth	398	4.31	2.06
5. Deciduous species	127	1.58	.91

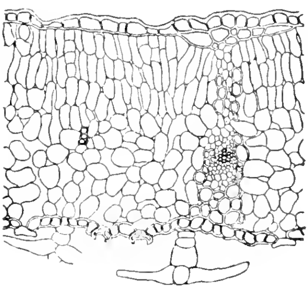
every case upon 10 separate leaves, except in *Adenostoma fasciculatum*, *Arctostaphylos tomentosa*, and *Quercus durata*, where the averages are of 40 to 50 separate leaves.

The following order has been determined upon in the descriptions: (1) general; (2) mesophyll; (3) epiderm; (4) stomata; (5) special features.

Broad-sclerophyll Forest.

Myrica californica.—(1) The thinnest of all the leaves studied. (2) Bifacial. Palisade tissue of one complete and one partial layer, occupying one-third of the mesophyll; in some places a suggestion of palisade layer next to the lower epiderm; sponge very loose. (4) Stomata on lower side only, slightly elevated. (5) A sheath of tannin-filled cells surrounds the bundles; occasional peltate glands in depressions on both surfaces.

Castanopsis chrysophylla (fig. 22).—(1) The specimens examined are of var. *minor*, from Monterey, and the leaves are probably somewhat more xerophytic in structure than those of the typical tree-form of the northern Coast Ranges. (2) Bifacial. Mesophyll dense; palisade tissue about four layers deep, occupying a little less than half the mesophyll, composed of rather crowded oval or nearly globular cells. (3) Epiderm, no special features; incomplete hypoderm on both sides, mainly related to veins. (4) Stomata on lower side only, slightly elevated, surrounded by collar-like ridges. (5) Tannin in cells surrounding bundles and in hypoderm; struts of mechanical tissue from epiderm to epiderm, following veins; multicellular trichomes covering lower surface, producing a golden fuzz.



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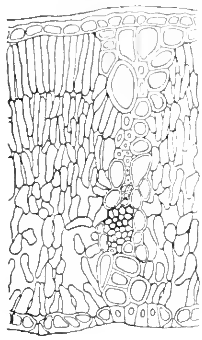

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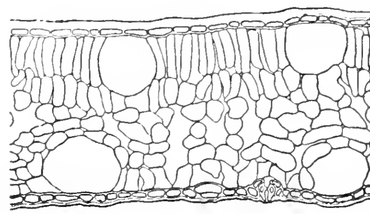

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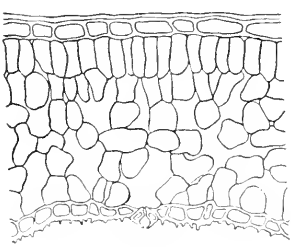
Fig. 22.—*Castanopsis chrysophylla:* section of leaf. ×125.
Fig. 23.—*Quercus agrifolia:* section of leaf. ×125.
Fig. 24.—*Umbellularia californica:* section of leaf. ×125.



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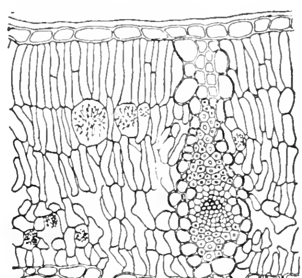

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Fig. 25.—*Arbutus menziesii:* section of leaf. ×125.
Fig. 26.—*Quercus durata:* section of leaf. ×125.

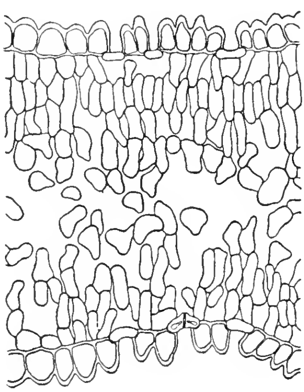
Quercus agrifolia (fig. 23).—(2) Leaf bifacial but not perfectly so. Palisade tissue about three to four layers deep, occupying about half the mesophyll and merging gradually into the sponge, the cells of which are mostly elongated perpendicularly to the surface, thus possessing palisade character; one or two incomplete palisade layers on lower side also. (4) Stomata on lower side only. (5) Struts of mechanical tissue as in *Castanopsis*, but more pronounced.

Quercus chrysolepis.—The specimens are from the shrubby chaparral form. Even so, they exhibit less of xerophytic character than the last, in that they are more perfectly bifacial and that the sponge is more typical. Otherwise they are essentially like those of *Q. agrifolia*.

Pasania densiflora.—(2) Bifacial. Palisade tissue about two layers in depth, occupying less than half the mesophyll; sponge not abundant, most of the space being taken up by groups of large, thin-walled parenchyma cells, apparently water-storage tissue. (3) A complete layer of hypoderm beneath the upper epiderm and resembling it; lower epiderm papillate. (4) Stomata on lower side only. (5) Struts of mechanical tissue like those of the other members of the family.

Umbellularia californica (fig. 24).—(2) Imperfectly bifacial. Palisade tissue two layers in depth, occupying half the mesophyll, and an imperfect layer next to the lower epiderm; large oil-cells in both palisade and sponge, many of those on the lower side being enlarged elements of the epiderm (84, p. 703). (4) Stomata on lower side only.

Arbutus menziesii (fig. 25).—(2) Bifacial. Palisade tissue of two complete rows, occupying one-third or more of the mesophyll. (3) Lower epiderm minutely papillate. (4) Stomata on lower side only, with small exterior chamber formed by a collar-like ridge. (5) Tannin very abundant, almost throughout the mesophyll.



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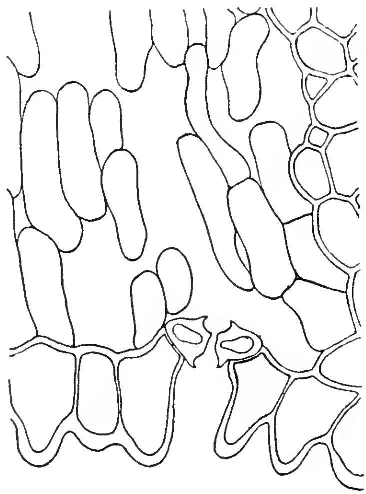

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FIG. 27.—*Dendromecon rigidum:* section of leaf. ×125.
FIG. 28.—*Dendromecon rigidum:* stoma. ×375.

CLIMAX CHAPARRAL.

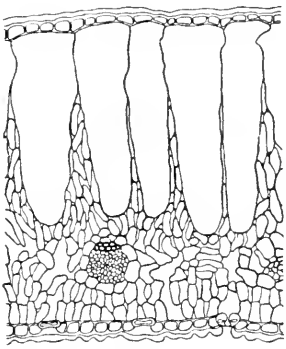
Quercus durata (fig. 26).—(2) Imperfectly bifacial. Palisade tissue about three layers deep, making half the mesophyll; sponge rather loose, but cells palisade-like. (3) Lower epiderm papillate. (4) Stomata on lower side only. (5) Tannin in lower epiderm and to some extent in upper; struts of mechanical tissue as in *Q. agrifolia*.

Berberis pinnata.—(2) Completely bifacial. Palisade tissue two layers deep, occupying half the mesophyll; sponge fairly typical. (4) Stomata on lower side only. (5) Struts of mechanical tissue associated with veins.

Dendromecon rigidum (figs. 27, 28).—(2) Almost perfectly isolateral, in correlation with its vertical placement. Palisade tissue on both sides of leaf, two perfect rows above, two imperfect ones below, rather loose; sponge central, occupying one-third of the mesophyll, loose. (3) Both upper and lower epiderm strikingly papillate. (4) Stomata numerous and large, on both surfaces, sunken in pits to the depth of the thickness of the epiderm. (5) Struts of mechanical tissue associated with veins.

Heteromeles arbutifolia.—(2) Bifacial. Palisade tissue about three layers deep, making less than half the mesophyll; sponge abundant, rather typical. (3) Lower epiderm papillate. (4) Stomata on lower side only, slightly sunken, with a small exterior chamber formed by a collar-like ring. (5) Tannin in bundle-sheath and almost throughout the mesophyll, abundant. Hypoderm has been reported by Gerard (see Solereder, 84, p. 303), but I have been unable to find any.

Adenostoma fasciculatum (plates 20B, 21A).—(1) Leaves needle-shaped, nearly terete, the morphologically upper side flattish, the lower roughly semicircular in cross-section; bundles arranged in a rough circle, the main one being opposite the middle of the upper side. (2) Palisade tissue about three layers in depth, equally developed on all sides, with wide gaps below the stomata; sponge central, loose, sharply differentiated from the palisade.



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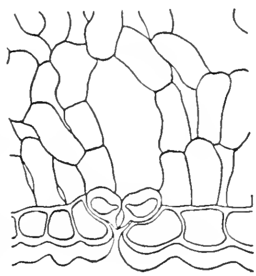

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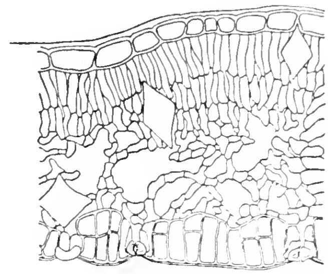

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FIG. 29.—*Xylothermia montana:* section of leaf. ×125.
FIG. 30.—*Xylothermia montana:* stoma. ×375.
FIG. 31.—*Rhamnus crocea:* section of leaf. ×125.

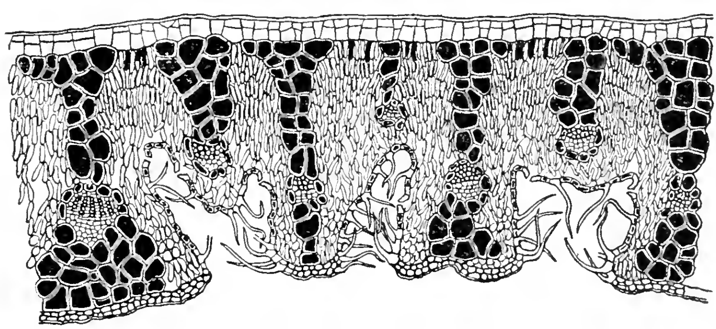


FIG. 32.—*Ceanothus cuneatus:* section of leaf; black indicates distribution of tannin. ×75.

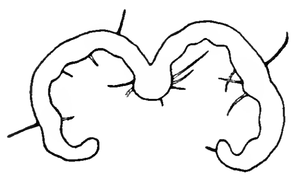
(3) Cuticle very thick, equally so on all sides. (4) Stomata on all sides, with exterior chambers of the depth of the cuticle, almost closed at the mouth and containing plugs of granular material. (5) Veins surrounded by heavy sheaths of large cells which are filled with tannin. Leaves from seedlings and sprouts are very different. These will be described in another section (p. 109).

Prunus ilicifolia.—(2) Imperfectly bifacial. Palisade tissue about four layers deep, making half the mesophyll, with one or two incomplete layers next to the lower epiderm; sponge scanty. (4) Stomata on lower side only. (5) Abundant tannin in bundle sheath.

Xylothermia montana (figs. 29, 30).—(2) A bifacial leaf of a novel type. Immediately below the upper epiderm is a single layer of enormous cells elongated perpendicularly to the surface, and extending from two-thirds to three-fourths of the distance to the lower epiderm. They resemble palisade tissue both in profile and cross-section, and may perhaps be regarded as a modified layer of such. They contain dense masses of tannin which completely fill the cavities, and which frequently come out whole or in pieces in the process of sectioning. According to authors quoted by Solereder (84, pp. 259–260), similar sacs in other members of the family may contain protein and other substances in addition to the tannin. Between the tapering lower ends of the tannin sacs are found the true palisade cells, which never reach the upper epiderm. Nearly all of the true mesophyll is palisade-like in character, the only differentiation being moderate looseness and irregularity near the lower epiderm. (3) Lower epiderm papillate and upper slightly so. (4) Stomata on lower side only, sunken to the depth of the epiderm, with small exterior chambers. (5) Tannin sacs: see above.

Rhamnus californica.—(2) Bifacial. Palisade tissue three to four layers deep, occupying slightly more than half the mesophyll; sponge loose. (3) Some cells of upper epiderm doubled, and occasionally one with an apparently gelatinized inner wall, as reported by Herzog (42). (4) Stomata on lower side only, not specialized. (5) Tannin in bundle-sheath; a rather thick covering of clustered hairs on lower surface.

Rhamnus crocea (fig. 31).—(2) Bifacial. Palisade tissue two to three layers deep, occupying half the mesophyll; sponge very loose. (3) Lower epiderm two to three times as thick as the upper, composed of cells elongated perpendicularly to the surface of the leaf, many of them being doubled; appearing like weakly developed water-storage tissue. (4) Stomata on lower side only, barely sunken. (5) Tannin in bundle-sheath.



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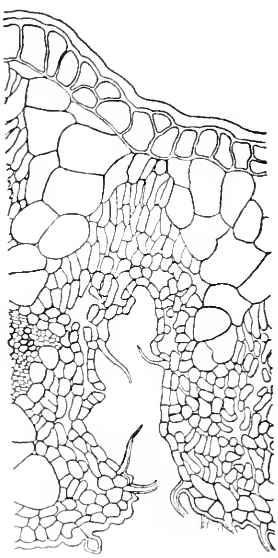

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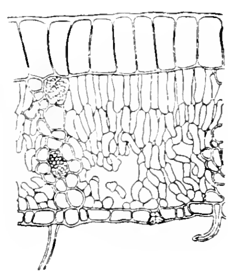

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FIG. 33.—*Ceanothus papillosus:* diagrammatic section of leaf. ×15.
FIG. 34.—*Ceanothus rigidus:* section of leaf, showing a single cavity and its surroundings; general features are like those of *C. cuneatus* (fig. 32). ×125.
FIG. 35.—*Ceanothus sorediatus:* section of leaf. ×125.

Ceanothus cuneatus (fig. 32).—(1) One of the thickest of the leaves studied. (2) Bifacial. Mesophyll very complex (Solereder, p. 886; Gemoll, 32). Palisade tissue about six layers deep, not continuous horizontally, occupying the areolæ between the closely anastomosing veins, the courses of which are prominently marked by strands of tannin cells; dense, but becoming looser and simulating sponge in center of leaf. Mesophyll extends to lower surface around the cavities (see below), in the lower half being of rather dense sponge nature, with a tendency toward palisade-form near the epiderm. (3) Upper epiderm partially and irregularly double, the inner cells mostly large.[1] Lower epiderm,

[1] Gemoll (32) states that all the cells of the upper epiderm have gelatinized inner walls, and says nothing of doubling. The interpretation given here seems not to be open to doubt, however. My material was killed and preserved in formalin-alcohol and cut by the celloidin method, while Gemoll obtained his from dried herbarium specimens.

between cavities, with one or two layers of thick-walled hypoderm behind it, the cuticle papillate. In the areolæ between the veins the lower epiderm is deeply invaginated to form cavities, extending through half the thickness of the leaf and frequently compound, whose entrances are often smaller than their interior diameters. The epiderm lining these is very thin, not cuticularized, and bears an abundance of hairs, which fill the cavities with

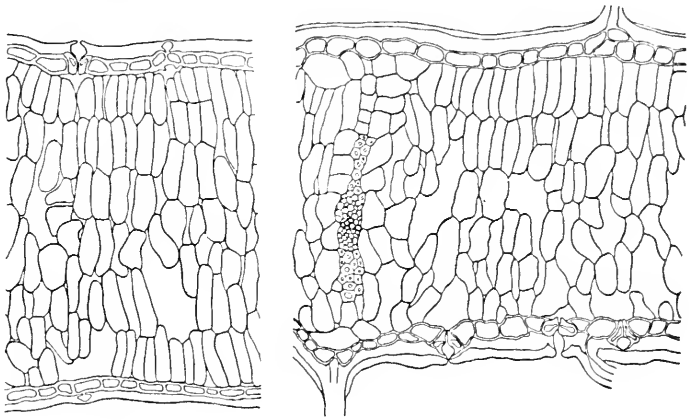

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Fig. 36.—*Arctostaphylos hookeri:* section of leaf. ×125.
Fig. 37.—*Arctostaphylos vestita:* section of leaf. ×125.

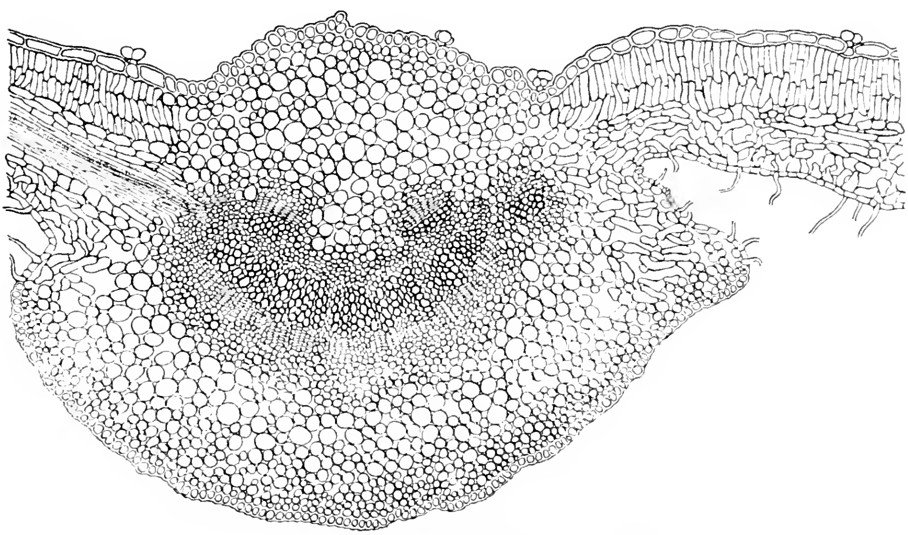

Fig. 38.—*Eriodictyon californicum:* section of leaf. ×75.

a dense felt. (4) The stomata are found within the cavities, and are raised above their immediate surroundings. (5) Tannin is very abundant: in sheath surrounding bundles and filling very large cells which in the region of the bundles are massed from epiderm to epiderm, the individual cells being many times larger than the palisades; also in the cells of the lower epiderm, where it lines the cavities, and in an occasional cell of the upper layer of the palisade tissue.

Ceanothus papillosus[1] (fig. 33).—(1) Leaf strikingly revolute. (2) Bifacial. Palisade tissue two to three layers deep, occupying one-half the mesophyll; sponge rather loose, and many of the cells palisade-like. (3) Upper epiderm making one-sixth to one-fifth the thickness of the leaf, composed of large cells filled with tannin; lower epiderm much thinner, undulate, the cells also containing tannin. (4) Tannin in bundle-sheath, collenchyma of midrib, and epiderm; sparse scattering of single hairs on both sides.

Ceanothus rigidus (fig. 34).—The description of *C. cuneatus* will answer for this species in almost every particular. The slight differences noted are the smaller proportional size of the entrances to the cavities and the greater elevation of the stomata above their immediate surroundings. Gemoll (32) gives an illustration of the cross-section of the leaf of *C. crassifolius*. It is very similar to *C. cuneatus* and *C. rigidus*. Probably all the species of the subgenus *Cerastes* have leaves of the same general character.

Ceanothus sorediatus (fig. 35).—(2) Bifacial. Palisade tissue two layers deep, occupying half the mesophyll; sponge rather loose. (3) Epiderm much like that of *C. papillosus*, but the upper is even more prominent, making from one-fourth to one-third the thickness of the leaf. (4) Stomata on lower side only. (5) Tannin abundant in bundle-sheath, collenchyma of midrib, upper and lower epiderm, and occasional palisade cells; very sparse hairy covering on lower surface.

Garrya elliptica.—(2) Bifacial. Palisade tissue about three layers deep, occupying half the mesophyll, the uppermost layer composed of cells that are shorter than the others and of twice the diameter;[2] sponge loose. (3) Upper and lower epiderm papillate; upper cuticle by far the thickest of all those examined. (4) Stomata on lower side only, very numerous and large, each surrounded by an imposing collar-like ridge. (5) Dense hairy covering on lower surface; isolated sclerenchymatous cells of various shapes in the mesophyll.

Arctostaphylos hookeri (fig. 36).—(2) Almost perfectly isolateral. Mesophyll composed entirely of palisade tissue—about seven layers—slightly denser on the morphologically upper side. (3) Cuticle very slightly thinner on the lower side. (4) Stomata on both surfaces, sunken to the depth of the epiderm, with a small exterior chamber nearly closed at the mouth. (5) Tannin almost throughout the mesophyll.

Arctostaphylos pumila.—Very similar to the last, but not so perfectly isolateral; palisade less dense in the lower half; stomata on lower side only.

Arctostaphylos tomentosa.—Essentially like *A. pumila*. According to Niedenzu (70), the stomata occur on both surfaces. My material does not confirm this, but such a difference would not be strange in so variable a species.

Arctostaphylos vestita (fig. 37).—Essentially like *A. pumila;* cuticle distinctly stratified.

Eriodictyon californicum (fig. 38).—(2) Bifacial. Palisade tissue very sharply differentiated, about four layers in depth, occupying half or a little more than half of the mesophyll; sponge loose. (3) Upper epiderm papillate, with an exceedingly thin cuticle; lower epiderm moderately invaginated between the veins, very thin here, not perceptibly cuticularized, on the ridges opposite the veins resembling the upper epiderm; a very deep invagination on each side of the very large midrib. (4) Stomata on lower side only, confined to the invaginated portions, slightly raised above their immediate surroundings. (5) A dense hairy covering on lower surface, not confined to the furrows, but best developed there.

Two species which belong to the broad-sclerophyll element of the redwood-forest undergrowth have been studied for the sake of comparison. These, with the other members of the group, range far north of California into the conifer forests of the Puget Sound region.

Gaultheria shallon.—(1) Much like species of *Arctostaphylos* in general appearance, but distinctly bifacial. (2) Palisade tissue one to two layers in depth, occupying one-third or a little more of the mesophyll; sponge rather typical, very loose. (3) Upper cuticle moderately thick, lower thin. (4) Stomata on lower side only, with a small exterior chamber with constricted opening. (5) Tannin in bundle-sheath, almost throughout mesophyll, and in upper and lower epiderm.

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[1] A recent visit to the locality of collection seems to indicate that the material studied is *Ceanothus dentatus* rather than *C. papillosus*. The two species are closely related.

[2] Apparently interpreted as hypoderm by Sertorius (see Solereder, 84, p. 433); but the cells contain chloroplasts and are plainly a part of the palisade.

Vaccinium ovatum (fig. 39).—(2) Bifacial. Palisade tissue two layers in depth, occupying one-third or less of the mesophyll, its cells very short and rounded; sponge very loose. (3) Cells of upper epiderm large, with a moderately thick cuticle; lower cuticle very thin. (4) Stomata on lower side only, very slightly elevated. (5) Tannin in bundle sheath and in the mesophyll, mainly the sponge-cells.

TABLE 14.—*Summary of structural characters.*

	Broad-sclerophyll forest (7 species).	Climax chaparral (19 species).	Total (26 species).	Redwood undergrowth (2 species).
Leaf more than 300 microns thick	1	12	13	2
Mesophyll:				
Bifacial	4	12	16	2
Imperfectly bifacial	3	4	7	...
Isolateral	...	3	3	...
Entirely palisade	...	2	2	...
More than 2 layers of palisade	3	15	18	...
Sponge central	...	2	2	...
Water-storage tissue	1	...	1	...
Epiderm:				
Partially double:				
Upper	...	3	3	...
Lower	...	1	1	...
Lower epiderm invaginated	...	3	3	...
Papillate:				
Upper	...	4	4	...
Lower	2	8	10	...
Upper cuticle more than 4 microns thick	1	13	14	2
Hypoderm:				
Upper side	2	...	2	...
Lower side	...	3	3	...
Stomata:				
Lower surface only	7	15	22	2
Both surfaces	...	4	4	...
Sunken	...	6	6	...
With exterior chamber	1	6	7	1
In furrows or cavities	...	3	3	...
Tannin:				
In bundle-sheath	2	9	11	2
In mesophyll	1	8	9	2
In epiderm	...	5	5	1
Mechanical tissue (struts)	4	3	7	...

The principal structural characters of the species described are summarized in table 14 by communities. From the data given, we may characterize the average Californian broad-sclerophyll leaf as follows:

It is moderately small (averaging 2 to 3 cm. in length), simple, unlobed, elliptic, and in a majority of cases entire and glabrous. Important groups are toothed, spiny-toothed, revolute, or pubescent on the lower or on both surfaces. The leaf is thick, averaging 314 microns, while the deciduous species studied average only 127 microns. The mesophyll is most commonly bifacial, though often imperfectly so, but a few are isolateral. The palisade tissue is several layers deep. The epiderm is nearly always single, and often papillate. The cuticle is very thick, the upper averaging 5.69 microns as against 1.58 microns in the deciduous species. In the case of the lower the difference is still greater: 4.43 microns and 0.91 microns. The stomata in a large majority are on the lower surface only. Many special features occur in their structure and distribution that are effective in decreasing water-loss. Tannin is abundant and widespread in bundle-sheath, mesophyll, and epiderm.

Divergences from Schimper's generalizations, quoted at the beginning of the chapter, are unimportant. The average Californian leaf is smaller than his statement implies; it tends toward the oval rather than the lanceolate in form, and vertical placement is less pronounced. Many special features are here described which do not appear in his account.

Comparing the two communities, we find that the broad-sclerophyll forest has uniformly much larger leaves, which are less often entire. The climax chaparral leaf averages 50 per cent thicker than the forest leaf; it includes all the isolateral and the majority of the imperfectly bifacial leaves, and its palisade tissue is more prominent, averaging 4 to 5 layers and 66 per cent of the mesophyll as against 2 to 3 layers and 43 per cent in the forest species. The chaparral leaves have a much thicker cuticle than those of the forest—nearly 100 per cent greater on the upper side and more than 150 per cent greater on the lower. The species with stomata on both surfaces, which are those with isolateral vertical leaves, are all of the chaparral. Special features protective against water-loss are almost entirely confined to the chaparral.

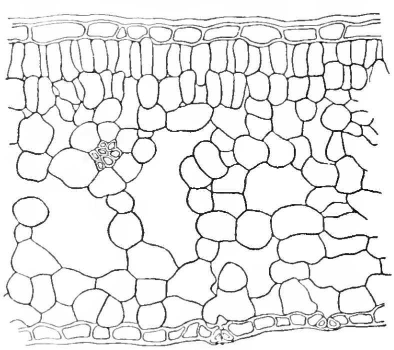


Fig. 39.—*Vaccinium ovatum:* section of leaf. ×125.

We see thus that the broad-sclerophylls, as compared with deciduous species, have a wealth of features of the kind that have been assumed to be a response to the moisture conditions of the habitat, and which are certainly effective in decreasing water-loss. Certain of the characteristics, such as spiny teeth, papillate epiderm, and presence of tannin, have no obvious relation to this or to any other habitat factor, either as to cause and effect or advantage. We see further that the chaparral species are in every way more fully provided with transpiration-decreasing features than are the forest species. The group from the redwood undergrowth is rather puzzling. In thickness of leaf the two species studied are surpassed by but three species of the chaparral; in thickness of cuticle they are superior to all the species of the forest and to many of the chaparral. The mesophyll, however, is decidedly suggestive of mesophytic influences. The habitat of these plants is far more mesophytic than that of the other broad-sclerophylls, and the xeromorphic construction of their leaves is a warning against the determination of the essential ecological nature of a plant by one structure alone. The commonness of this type of leaf in the family Ericaceæ, apparently regardless of habitat, is too well known to require comment.

EFFECTS OF ENVIRONMENTAL CONDITIONS UPON LEAF STRUCTURE.

It is commonly assumed that moisture and light influence powerfully the structure of leaves, especially the thickness and character of the mesophyll and epiderm. Many have essayed to separate the effects of the two factors, not always with success. While it is impossible in such a field study as the present to make a close analysis of cause and effect, any correlation of structural differences with accurately measured habitat factors is of value, and therefore the following brief study is presented.

Three stations in the series at Jasper Ridge (p. 33) were selected, Nos. 4, 3, and 7 representing respectively the *Adenostoma*, the *Arctostaphylos*, and the *Quercus agrifolia-Arbutus* communities. A summary of the moisture and light conditions of each station is presented in table 15. The figures are derived from the data given in an earlier section (p. 42). Soil-moisture is expressed in per cent of dry-soil weight, and the figure is an average of a series of six monthly determinations at two depths (10 cm. and 30 to 50 cm.) during the dry season from June 15 to October 31, 1913. Evaporation is given in cubic centimeters of daily loss from a standard atmometer, determined weekly, and averaged for practically the same period as the soil-moisture readings. Light is expressed as a decimal of the full illumination. The readings were made as close together as possible in time, at midday of August 17, 1917. The species chosen for study were the three most prominent chaparral shrubs of the vicinity, *Adenostoma fasciculatum*, *Arctostaphylos tomentosa*, and *Quercus durata*. The natural habitat of these species is of the character of stations 4 and 3, but they grow occasionally as interlopers in the forest, which is represented by station 7, and thus give opportunity for comparison. The material was collected from widely separated plants within a given association, preserved in formalin-alcohol and cut in paraffin. In making the measurements, 10 separate leaves were used and 5 measurements made upon each leaf. Every figure given is therefore an average of 50 separate measurements.

The habitat analysis shows that the stations, in the order as given, are progressively more favorable as regards moisture conditions, both in water-content and in evaporation, and progressively more deficient in light. Stations 3 and 4, however, are rather similar in every factor, while station 7 is quite different. It is not surprising, therefore, to find striking structural divergence between stations 3 and 4 on the one hand and station 7 on the other, and far less consistent differences between stations 3 and 4. The leaf is thinnest

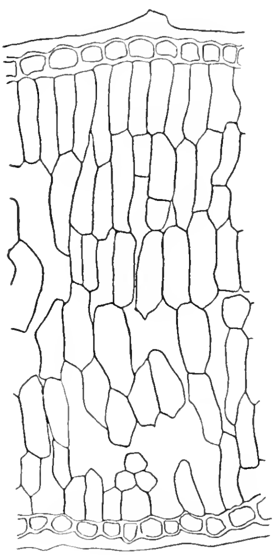
TABLE 15.—*Effect of habitat upon leaf structure.*

	Station 4. Adenostoma chaparral.	Station 3. Arctostaphylos chaparral.	Station 7. Quercus agrifolia-Arbutus forest.
Habitat:			
Light:			
Sun	0.75	0.69	0.56
Shade	0.21	0.04	0.07
Soil-moisture, p. ct.	3.24	3.38	3.81
Evaporation, c. c.	30.1	28.4	22.7
Leaf-structure:			
Adenostoma fasciculatum:			
Leaf, microns	541	574	475
Upper cuticle, microns	10.10	10.65	11.00
Lower cuticle, microns	10.26	11.00	4.64
Arctostaphylos tomentosa:			
Leaf, microns	371	366	250
Upper cuticle, microns	9.77	9.06	6.94
Lower cuticle, microns	9.36	14.30	7.67
Quercus durata:			
Leaf, microns	233	198	193
Upper cuticle, microns	3.38	2.77	2.55
Lower cuticle, microns	4.05	3.23	2.66

in station 7, and the same is true of the lower cuticle, the differences in the latter case being especially noticeable. In the case of the upper cuticle the differences in *Arctostaphylos* and *Quercus* are less, and in *Adenostoma* there is reversal, the mesophytic station 7 showing a cuticle slightly thicker than the others. There are also differences apparent in the mesophyll, especially in *Arctostaphylos*. In this species the sections from stations 3 and 4 are barely distinguishable, but these two differ strikingly from station 7. Such differences can not be expressed numerically, but are very evident in drawings (figs. 40 and 41). In the leaf from station 4, the dense palisade extends from epiderm to epiderm, being slightly looser below, with here and there a tendency toward sponge character. In that from station 7 the palisade is but two layers deep, and there is a distinct region of sponge tissue. *Quercus* and *Adenostoma* from the three stations show far less striking differences.

We conclude, therefore, that increased thickness of leaf and of cuticle, increased development of palisade tissue, and decrease of sponge coincide with decrease of moisture and increase of light. Further than this we can not certainly go. The natural assumption is that moisture is the controlling factor rather than light, which may have an indirect effect.

Evidence that this assumption is well founded may be obtained from that unusually interesting plant *Adenostoma fasciculatum*, in the remarkable type of leaf that is found upon seedlings and stump sprouts and to a slight degree on mature plants growing in mesophytic situations. Prints of these, with the ordinary type for comparison, are given in plate 21B. The differences in structure are no less striking than in form (plate 20, B, C, D). The sprout or seedling



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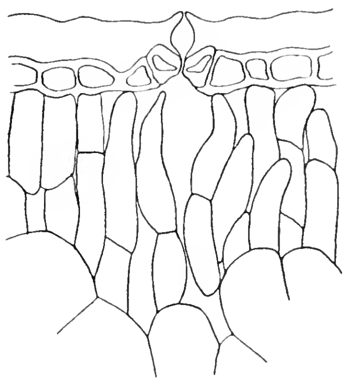

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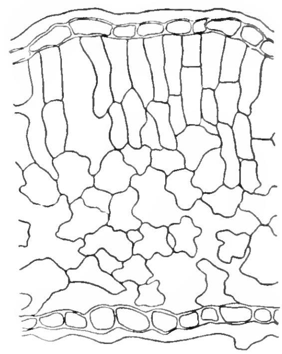

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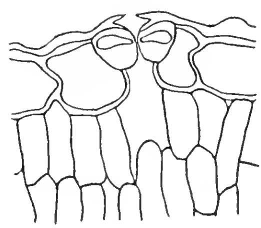

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FIG. 40.—*Arctostaphylos tomentosa:* section of leaf from a xerophytic habitat (station 4, Jasper Ridge). ×125.
FIG. 41.—*Arctostaphylos tomentosa:* section of leaf from a mesophytic habitat (station 7, Jasper Ridge). ×125.
FIG. 42.—*Adenostoma fasciculatum:* stoma of normal xerophytic specimen. ×375.
FIG. 43.—*Adenostoma fasciculatum:* stoma of leaf from stump sprout. ×375.

leaf is a flat isolateral structure, averaging 300 microns in thickness, with the veins in a single plane after the manner of ordinary leaves. The mesophyll is loose, especially the central sponge, and both palisade and sponge cells are short and rounded. The epidermal cells are very large, thin-walled, and turgid. The cuticle is very thin—1.5 microns as contrasted with 9.73 microns in the ordinary leaf of the species. The stomata occur on both surfaces. They still possess the exterior chamber, but this is very shallow and open-mouthed (figs. 42, 43).

We may explain these remarkable structural changes—broadening of the leaf to form a flat blade, loosening of the mesophyll, loss of character in the palisade, reduction of cuticle—after a fashion by stating that the abnormal leaf type is an ancestral character to which the plant reverts in its juvenile stage. This in itself is begging the question, and doubt is cast upon its adequacy by the fact that the flat leaf sometimes appears in mature individuals in mesophytic situations (plate 21A, *b*). Light can not be operative here, since it is at maximum intensity where sprouts and seedlings are found, and observed changes due to increased intensity are invariably in the opposite direction. Moisture as the governing factor seems entirely adequate. New stump sprouts, even in the midst of the dry season, have an exceptional advantage as to water, since they may draw upon an absorbing system which formerly supplied a complete mature shrub. The large size of leaves upon stump sprouts and their mesophytic structure are well-known phenomena, and are characteristic of other chaparral species besides *Adenostoma*. As to seedlings, germination and early growth take place at a time of year when soil-moisture is abundant and evaporation low, and the plant supplements this advantage by immediately sending down a taproot to a considerable depth. The occasional occurrence of the flat leaf upon mature individuals in mesophytic situations is the final argument. It may well be that the mesophytic leaf with its distinctive form and structure points back to a mesophytic ancestry for the species, which would help to bring it into harmony with the majority of the members of its family, among which it is decidedly an anomaly. Finally, since moisture seems adequate as a cause of variation in the form and thickness of the leaf of *Adenostoma* and in the character of its mesophyll and cuticle, it is reasonable to assume that it is the controlling factor in the other species where the same differences are present but less striking.

COMPARATIVE TRANSPIRATION-RATE.

In the summer of 1917 I made a brief study to determine the actual transpiration-rate of two or three of the important broad-sclerophyll species. The results were somewhat puzzling, though consistent enough among themselves, and it is therefore the better part of valor to withhold them in the main for further investigation. One or two points were clearly brought out, however, which are worth stating here.

The study was made by the simple potometer method—the placing of branches in bottles of water, which were weighed at the beginning and end of the experiment. The mouths of the bottles were plugged with cotton, which was kept perfectly dry. One or two which became wet during the experiment were discarded. The species used were *Adenostoma fasciculatum*, *Arctostaphylos tomentosa*, and *Arbutus menziesii*. Ten shoots of each of the first two were cut in station 10 (*Adenostoma* consociation; see p. 41 for environment), placed in bottles and weighed. Five of each species were left in station 10 and the rest were placed in station 7 (*Quercus agrifolia-Arbutus* association, p. 38). In station 7, 10 branches each of the same species were cut, and in addition 10 of *Arbutus menziesii*, and half of each set were left in station 7 and the others taken to station 10. The experiment was allowed to run for about 48 hours, from August 24 to August 26. The branches were pressed between driers, and the areas of the leaves of *Arctostaphylos* and *Arbutus* were later determined with a planimeter. In the case of *Adenostoma*, with its terete leaves, a different and less exact method was necessary. Each branch was stripped of its leaves and these counted. Then 20 were selected at random, placed in boiling water to restore them approximately to their original size, and measured accurately as to length and diameter. The area was computed as a cylindrical surface, the average of the 20 taken, and this applied to the total number of leaves on the shoot. The total losses recorded for each shoot were reduced to the amount per square decimeter of surface. So much of the results as are worth giving at present are seen in tables 16, 17, and 18.

TABLE 16.—*Loss per square decimeter, station 10.*

	c. c.
Adenostoma (average of 5 shoots)	5.32
Arctostaphylos (average of 5 shoots)	6.68
Arctostaphylos (both surfaces considered)	3.34

It is shown that when the stoma-bearing surface alone is considered, the loss per unit is less in *Adenostoma;* but if both surfaces of the leaf are considered in *Arctostaphylos*, as we must fairly do, the relation is reversed. It would seem, therefore, that the *Adenostoma* leaf is the more effective in reducing water-loss so far as the actual stoma-bearing surface is concerned, but that *Arctostaphylos* compensates for this by the entire absence of stomata (at least in the plants studied; see p. 104) over half its leaf-surface. The more perfect xerophytism of *Adenostoma* can not be explained, therefore, upon the basis of cuticular and stomatal regulation; and this is confirmed by the descriptions presented in the last section, in which these structures are seen to be very similar in the two species. We may fall back upon the hypothesis that the total leaf-area is less in *Adenostoma* than in *Arctostaphylos*, plants of equal size being considered; individuals of the two species are apt to be so when growing together. The general appearance would indicate this, especially the small size of the leaves of *Adenostoma*, and confirmation is obtained from the fact that the average leaf-area of the shoots used in the experiment (both surfaces considered in *Arctostaphylos*) was 75 per cent greater in *Arctostaphylos*. Of course, this is merely a rough approximation, but since care was taken to select branches as nearly alike as possible, it doubtless indicates the truth.

For comparison with *Arbutus* it is necessary to use the shoots of all species that were cut in station 7 and left there (table 17).

TABLE 17.—*Loss per square decimeter, station 7.*

	c. c.
Adenostoma (average of 5 shoots)	2.77
Arctostaphylos (average of 5 shoots)	3.96
Arctostaphylos (both surfaces considered)	1.98
Arbutus (average of 5 shoots)	3.69
Arbutus (both surfaces considered)	1.85

The two shrubs show the same relations here as in station 10. *Arbutus* seems to be slightly more effective in reducing water-loss than *Arctostaphylos*, and therefore more effective than *Adenostoma* per unit total surface. However, the average total leaf-surface per shoot was 38 per cent greater than *Arctostaphylos* and thus far greater than *Adenostoma*, indicating that even for a plant of equal size the total leaf-surface would be greater; and there is the further fact of the tree stature of *Arbutus*. The conclusion seems to be that it is not so much differences in cuticular or stomatal effectiveness that make the difference in drought resistance as it is the total leaf-area exposed in plants of approximately equal size, the separate elements in this character being number and size of leaves.

One other point may be brought out. Table 18 exhibits the difference in evaporation-rate which appears in the same species growing in the two habitats, due fundamentally to differences in the environmental conditions.

TABLE 18.—*Loss per square decimeter, station 7.*

	c. c.
Adenostoma (station 7)	2.77
Adenostoma (station 10)	5.32
Arctostaphylos (station 7)	1.98
Arctostaphylos (station 10)	3.34

In *Arctostaphylos* the rate in the xerophytic station is 70 per cent greater than in the other, while in *Adenostoma* the difference is nearly 100 per cent. The study of the transpiration of these plants is one of the most promising fields for further investigation.

APPENDIX.

ANNOTATED LIST OF BROAD-SCLEROPHYLLS AND ACCOMPANYING SPECIES.

In listing the species which make up the broad-sclerophyll vegetation of California, a separation into groups will be convenient. The first great division is into dominants and secondary species; both classes may conveniently be subdivided.

THE DOMINANTS.

Under this head I would include all the true forest and brush-forming species—those which give to the type its characteristic physiognomy. Although the majority are strikingly similar in ecological character, they present great floristic diversity. The first two lists include 74 broad-sclerophylls, representing 23 genera and 13 families. In all lists species restricted to the Californian islands have been excluded. Another group of broad-sclerophylls, mentioned in the last chapter, comprises the half-dozen species which form an important part of the undergrowth of the northwestern conifer forests. These are *Berberis nervosa* Pursh, *Pachystima myrsinites* Raf., *Rhododendron californicum* Hook., *Gaultheria shallon* Pursh, and *Vaccinium ovatum* Pursh.

The following list includes all the species that are of importance in the composition of the broad-sclerophyll forest. They are few in number, and most are of wide range within the Californian region. Some are themselves not broad-sclerophylls, but are deciduous; these have been grouped together at the end of the list. A number of the species, too, when growing in relatively unfavorable situations, take the shrub form and in some cases are more important thus than as trees. In a few instances the shrubby form has been separated by taxonomists as a variety.

LIST I.—ARBORESCENT SPECIES.

EVERGREEN.

1. *Myrica californica* Chamisso. Wax myrtle. Immediate coastal region from Puget Sound to Los Angeles County. Of subordinate importance as a forest tree.

2. *Castanopsis chrysophylla* (Hook.) A. DC. Golden chinquapin. As a forest tree it occurs in western Oregon and in the mountains of northwestern California southward to Mendocino County. In the latter region it is a member of the mixed broad-sclerophyll-conifer forest. It is also frequently associated with the redwood. Var. *minor* A. DC. is a shrub closely resembling *C. sempervirens* (see No. 17). It is characteristic of the Coast Ranges, extending southward to Monterey, while *C. sempervirens* belongs rather to the Sierras. It is a frequent member of the conifer forest chaparral in the north Coast Ranges, and appears also in the climax chaparral.

3. *Quercus agrifolia* Nee. Coast live oak. Outer Coast Ranges and valleys near the coast, from Mendocino County to Mount San Pedro Martir in Lower California. The most important live oak, and probably the most important of the genus, within its range. Covers hillsides, especially north-facing slopes, with dense forest; also commonly in open park-like growth in valleys of the coast range; in such places attaining its largest size, and frequently associated with *Q. lobata*. Almost invariably tree-like in form, the only notable exceptions being the bushy contorted specimens in exposed situations near the shore.

4. *Quercus chrysolepis* Liebm. Mountain live oak. In southwestern Oregon and throughout the California mountains west of the high Sierras and the desert, except the lowest foothills; south to Mount San Pedro Martir in Lower California. The most widely distributed and most important of the live oaks of California, being the dominant member or one of two or three dominants in the broad-sclerophyll forest wherever it occurs. Very frequent in chaparral form, sometimes in rather tall pure growth on north slopes, forming ' dwarfforest."

5. *Quercus engelmanni* Greene. Engelmann oak. Of limited range; in southern California from Los Angeles County to the Mexican boundary, occupying a belt 80 km. wide, distant 25 to 30 km. from the coast. Important within its limited range. Barely evergreen.

6. *Quercus wislizeni* A. DC. Interior live oak. From Mount Shasta southward through the Sierra foothills and the Coast Ranges to Mount San Pedro Martir in Lower California; rarely, though occasionally, near the coast. Much less important as a forest tree than *Q. chrysolepis*, and characteristic of less mesophytic situations; occurs frequently in open growth with *Q. douglasii* on the lowest foothills. The shrubby form, var. *frutescens* Engelm., is very common in the climax chaparral.

7. *Pasania densiflora* Oerst. Tan-bark oak. Southwestern Oregon to the Santa Ynez Mountains in the Coast Ranges, and to Mariposa County in the Sierras. Characteristic of the mixed forest of the interior mountains of northern California; also commonly associated with the redwoods. The shrubby form, var. *echinoides* Jepson, is a member of the conifer-forest chaparral in northern California.

8. *Umbellularia californica* (H. and A.) Nutt. California laurel. Southwestern Oregon, southward through the Coast Ranges and Sierras to southern California. Characteristically a tree of the mesophytic forests, especially addicted to steep north slopes, ravines, and stream-banks. Sometimes shrubby, forming an unimportant part of the chaparral in the more mesophytic situations, especially in the extreme southern portion of its range.

9. *Arbutus menziesii* Pursh. Madroño. Southwestern British Columbia; through the coast region of Washington and Oregon; mountains of northern California; southward in the Sierras to Tuolumne County, and in the Coast Ranges to Los Angeles County. An exceedingly important tree of the broad-sclerophyll forest. Largest in northwestern California, where it accompanies the redwoods; in the central Coast Ranges second in importance to the live oaks, with them forming the bulk of the north-slope forests; decreasing southward in size and abundance, both in Coast Ranges and Sierras.

DECIDUOUS.

10. *Quercus douglasii* H. and A. Blue oak. Low foothills and valleys from Mendocino County to the upper Sacramento Valley, southward to the Liebre Mountains and the San Fernando Valley. Usually in open growth on the lowest foothills; sometimes pure, sometimes with *Pinus sabiniana* or *Quercus wislizeni.* Rarely associated with the broad-sclerophyll trees; the most xerophytic of the California oaks. Its relation to the chaparral is treated on page 79.

11. *Quercus garryana* Dougl. Garry oak. North Pacific States, extending southward in California along the Coast Ranges; abundant as far as Trinity County; occasional to the Santa Cruz Mountains. Not very important in California as a forest tree. In the northwestern portion, however, it forms dense pure thickets 2 or 3 meters high in the forest region.

12. *Quercus kelloggii* Newb. California black oak. Corresponding in range rather closely to *Quercus chrysolepis*, and a common companion to it in the forest. Occasionally, in shrub form, it makes a part of the conifer-forest chaparral.

13. *Quercus lobata* Nee. Valley oak. Valleys and foothills from Shasta County to Los Angeles County. Included here because it frequently forms park-like mixed forest with *Q. agrifolia.*

14. *Acer macrophyllum* Pursh. Broadleaf maple. Coast Ranges and Sierras, south to the San Bernardino Mountains. A frequent companion to the broad-sclerophyll trees in the more mesophytic localities.

15. *Æsculus californica* Nutt. California buckeye. Coast Ranges from Mendocino County to San Luis Obispo County; Sierra foothills. A common inhabitant of north-facing slopes in the foothills, growing with the live oaks; sometimes forming dense pure thickets.

The species of the next list are the shrubs that make up the chaparral, which in extent and in number of species and of individuals is far more important than the broad-sclerophyll forest. A further point of contrast is the far greater number of species in the chaparral which have a decidedly restricted range. To complete the picture, the following species from List I should be added, since in shrub form they have a more or less important place in the chaparral:

Castanopsis chrysophylla minor.
Quercus chrysolepis.
Quercus garryana.
Quercus wislizeni frutescens.
Pasania densiflora echinoides.

Considering the region as a whole, 4 genera, representing as many families, are of paramount importance in the chaparral. These are *Quercus*, *Adenostoma*, *Ceanothus*, and *Arctostaphylos*. They are widely different in the number of species representing them. *Adenostoma*, with the most important single species, includes 2; *Quercus* has 6 that are strictly chaparral forms; while in *Arctostaphylos* and *Ceanothus* I have listed 18 and 25, respectively. The treatment of the last two genera is of necessity unsatisfactory, since there is disagreement among taxonomists upon the fundamental questions of specific limits and relationships. In both genera there are groups of forms which are regarded by some authors as constituting single variable species. Within a group there are several forms which may be species, varieties, or merely ecological variants. It seems better for the present purpose, in doubtful cases, to consider the larger unit as the species, rather than to attempt to maintain a number of so-called species, sometimes poorly defined, of uncertain range, often known only from the type locality. It is not denied that these variant forms are of the greatest ecological interest and importance. At the present time, however, our knowledge of them is in every way insufficient to make adequate discussion possible. In the treatment of each genus I have, so far as possible, followed the author who has given the most recent and complete taxonomic account of the group concerned. These are Trelease (89) in *Ceanothus* and Abrams (2) in *Arctostaphylos*. In both cases I have omitted a number of species of uncertain validity or range.

In the list below I have attempted to indicate as accurately as has been possible to determine, from personal observation, literature, and herbaria, the range and degree of importance of each species of the chaparral. In the case of the most important one, *Adenostoma fasciculatum*, the range has been plotted on a map (plate 3). This is fairly accurate, since it is based on a careful and widely extended field study, supplemented by examination of literature and herbarium records, and by notes from a number of persons possessing a wide acquaintance with the vegetation of California. These sources together yielded a total of about 250 known localities.

List II.—Obligate Shrubs.

BETULACEÆ.

16. *Corylus rostrata* Ait. var. *californica* A. DC. Hazelnut. Central and northern Coast Ranges and Sierra Nevada. A rather unimportant constituent of the conifer-forest chaparral; occurs more commonly as undergrowth in mesophytic forest. Deciduous.[1]

17. *Castanopsis sempervirens* (Kellogg) Dudley. Golden chinquapin. From the southern Cascades along the Sierras, southward to Mount San Jacinto. Characteristic of the conifer-forest chaparral of the higher altitudes.

18. *Quercus breweri* Engelm. Brewer oak. Inner Coast Ranges from Mount Yolo Bolly north; Sierra Nevada to the Kern River region. Forms extensive thickets at middle altitudes. A member of the conifer-forest chaparral. Deciduous.

19. *Quercus dumosa* Nutt. Scrub oak. From the region of Mount Shasta to Lower California (lat. 31°); on the Coast Ranges and Sierra Nevada. Most abundant in the coastal region of southern California. A very important member of the climax chaparral, ranking with certain species of *Arctostaphylos* and *Ceanothus*, next to *Adenostoma*. Barely evergreen.

20. *Quercus durata* Jepson. Scrub oak. Closely related to the last. Range not satisfactorily determined, but apparently covering the middle Coast Ranges from the Santa Lucia Mountains north to Mendocino County and the Napa Range, and probably to the Trinity Mountains. Reported from Stanislaus National Forest in the Sierra Nevada. Similar in status to the last.

21. *Quercus sadleriana* R. Br. Confined to the mountains of southwestern Oregon and northwestern California. Forms pure thickets, probably successional. Barely evergreen.

22. *Quercus vaccinifolia* Kellogg. Huckleberry oak. Inner north Coast Ranges from Mount Shasta to Trinity County; throughout the higher forest region of the Sierra Nevada. A member of the conifer-forest chaparral; also occurring as undergrowth in the subalpine forests.

BERBERIDACEÆ.

23. *Berberis pinnata* Lag. California barberry. Central Coast Ranges. Sometimes in the chaparral; occasionally in the oak forests. Unimportant.

PAPAVERACEÆ.

24. *Dendromecon rigidum* Benth. Bush poppy. Of general distribution; from Shasta National Forest southward through Coast Ranges and Sierras, reaching Mount San Pedro Martir in Lower California; records scarce north of Sonoma and Napa Counties. A widely distributed and characteristic member of the climax chaparral, though nowhere abundant; its bright yellow flowers contribute a pleasing touch of color here and there.

ROSACEÆ.

25. *Heteromeles arbutifolia* (Poir.) Roem. Christmas berry; California holly; tollon (pronounced "toyon"). Coast Ranges and Sierra Nevada, and through southern California and Lower California to the Cape region. A characteristic member of the climax chaparral; not often abundant, but seemingly so because of its fine clusters of red berries and because it usually overtops its neighbors. Sometimes attains tree stature, but retains its shrub form. More tolerant of shade than most of its chaparral companions; therefore frequently found in the oak forest.

26. *Amelanchier alnifolia* Nutt. Service berry. Has the widest distribution of all the species occurring in the chaparral, ranging from Alaska to Mount San Pedro Martir in Lower California, east to Michigan, Nebraska, Colorado, and New Mexico; in California occurring in the Coast Ranges from San Francisco Bay northward, in the Sierras and the higher mountains of southern California. A rather frequent member of the conifer-forest chaparral. Deciduous.

27. *Cercocarpus betulæfolius* Nutt. Birch-leaf mahogany. Throughout the foothills and lower mountains of California. A common and frequently abundant member of the climax chaparral, especially in the more mesophytic situations. Often gregarious on north slopes, the groups in seed time showing from a distance as white patches.

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[1] Unless otherwise noted, species are evergreen in leaf habit.

28. *Cercocarpus ledifolius* Nutt. Mountain mahogany. Ranging widely over the western States, but not important as a member of the chaparral. Occurs sparingly in the chaparral of the San Bernardino Mountains and other southern California ranges, and in the Sierras, but mainly on the east slope.

29. *Adenostoma fasciculatum* H. and A. Chamise; grease-wood (the latter name, though frequent, is unfortunate, as it has been commonly applied to other shrubs, totally unrelated, of the western United States). Range shown in detail on map (plate 3). Its occurrence near Hershey in the Sacramento Valley, and other facts, seem to indicate that it formerly had a more widely extended range (see p. 79). The most abundant species and most important in every way of the shrubs of the climax chaparral. Usually in pure growth or nearly so over extensive areas, occupying the less mesophytic situations, which greatly predominate in the chaparral region. Pure growth is commonly known as "chamisal." Easily recognized at a distance, when growing in mass, by its characteristic color-tone, which varies according to the time of year. Its general shade is gray-green, but in June this is whitened by the profusion of spiræa-like flower panicles, and through the remainder of the summer and autumn turned to rich brown by the equally abundant clusters of withered flowers and achenes.

30. *Adenostoma sparsifolium* Torr. Yerba del Pasmo. San Jacinto and Santa Monica Mountains to Lower California; also in Santa Ynez Mountains. An interesting and handsome species of limited range and abundance; occurs in the same sort of situations as the last.

31. *Prunus demissa* (Nutt.) Walp. Western choke cherry. Rocky Mountains to the Pacific States and British Columbia. In California, a widely distributed but unimportant member of the conifer-forest chaparral; commoner in stream-bank thickets. Deciduous.

32. *Prunus emarginata* (Dougl.) Walp. Bitter cherry. Range similar to last; not so far eastward, but extending south to Mount San Pedro Martir in Lower California. In California an important member of the conifer-forest chaparral, frequently forming extensive thickets. Deciduous.

33. *Prunus ilicifolia* (Nutt.) Walp. Holly-leaf cherry; islay. South Coast Ranges, from the region of San Francisco Bay to Lower California. A frequent member of the climax chaparral; when shrubby closely resembling *Rhamnus crocea*. In more mesophytic situations it often attains small tree size, with a trunk 3 dm. thick, in such cases resembling *Quercus agrifolia* so closely in habit and leaf-form as to be distinguishable with difficulty.

34. *Prunus subcordata* Benth. Western plum. Southern Oregon southward, in the Coast Ranges to the Mount Hamilton Range, in the Sierras to the Kern River region. An unimportant member of the conifer-forest chaparral. Deciduous.

CÆSALPINACEÆ.

35. *Cercis occidentalis* Torr. Redbud. Foothills of Sierras and Coast Ranges southward to San Diego County, eastward to western Texas. Frequently a stream-bank shrub; occasionally a member of the chaparral; in the Cuyamaca Mountains seen in pure thicket growth on a northeast slope. Deciduous.

LEGUMINOSÆ.

36. *Xylothermia montana* (Nutt.) Greene [*Pickeringia montana* Nutt.]. Chaparral pea. Coast Ranges from Mendocino and Lake Counties southward; Sierra Nevada, from Mariposa County southward; var. *tomentosa* Abrams in mountains of southern California and Lower California. A widely distributed but not abundant member of the climax chaparral.

RUTACEÆ.

37. *Cneoridium dumosum* (Nutt.) Hook. f. San Diego County and northern Lower California. Climax chaparral.

ANACARDIACEÆ.

38. *Rhus integrifolia* (Nutt.) B. and H. Mahogany sumach. Santa Barbara to Mount San Pedro Martir and Magdalena Bay, extending eastward to the desert slopes of the Cuyamaca Mountains.

39. *Rhus laurina* Nutt. Laurel-leaf sumach. Santa Ynez Mountains to the San Gabriel Range, southward to northwestern Lower California, mainly near the coast. Usually not abundant, but conspicuous by reason of its light-green foliage.

40. *Rhus ovata* Wats. Ovate-leaved sumach. Santa Ynez Mountains to San Bernardino and San Jacinto Ranges, south to Mount San Pedro Martir in Lower California.

ACERACEÆ.

41. *Acer glabrum* Torr. Dwarf maple. Southeastern Alaska to Montana, Colorado, western Nebraska, New Mexico; west to California, where it ranges from the Oregon line southward to northern Trinity County, throughout the middle altitudes of the Sierras, and in the San Bernardino and San Jacinto Ranges. A mesophytic shrub, sometimes forming an unimportant part of the conifer-forest chaparral. Deciduous.

RHAMNACEÆ.

42. *Rhamnus californica* Esch. (including var. *rubra* Trelease and var. *tomentella* Brew. and Wats.). Coffeeberry. Coast Ranges and Sierra Nevada, south to Mount San Pedro Martir in Lower California. A frequent member of the climax chaparral, occurring also in more mesophytic situations such as the oak forest. Var. *tomentella* extends eastward into Arizona and New Mexico; var. *rubra* is deciduous, belonging rather to the conifer-forest chaparral.

43. *Rhamnus crocea* Nutt. (including *R. ilicifolia* Kellogg). Evergreen buckthorn; red-berry. Siskiyou County southward in the Coast Ranges and Sierra Nevada, extending to Mount San Pedro Martir in Lower California; eastward to Providence Mountains, California, and into Mexico and Arizona. A frequent member of the climax chaparral.

44. *Ceanothus cordulatus* Kellogg. Snowbrush. Forested northern Coast Ranges and throughout the higher Sierra Nevada forest regions; higher mountains of southern California and Lower California to Mount San Pedro Martir; mountains of Nevada according to Mrs. Brandegee (10). One of the most important constituents of the conifer-forest chaparral, covering extensive areas pure or mixed with other species. As is natural, considering its successional status, it is also found abundantly as undergrowth in the coniferous forest.

45. *Ceanothus crassifolius* Torr. Santa Ynez Mountains to the San Gabriel and San Bernardino Ranges, south to northern Lower California. An important constituent in its range of the climax chaparral, conspicuous because of its grayish-green foliage.

46. *Ceanothus cuneatus* Nutt. Wedge-leaf ceanothus. Omnipresent in the lower altitudes of the California mountains; extending northward into southern Oregon and probably southward into Lower California. One of the three or four most abundant species in the climax chaparral region. It comes up in great numbers after fire, and its presence in abundance usually indicates recent disturbance.

47. *Ceanothus dentatus* T. and G. Outer Coast Ranges from the Santa Cruz Mountains to Santa Barbara County.

48. *Ceanothus divaricatus* Nutt. (including var. *eglandulosus* Torr.). Monterey County south to the San Bernardino Range, Cuyamaca Mountains, and Lower California; also in the central and southern Sierras. An important shrub in the climax chaparral of the southern California mountains.

49. *Ceanothus diversifolius* Kellogg. Central Sierras, in the yellow pine belt. A creeping shrub, growing beneath the pines, not forming brush.

50. *Ceanothus foliosus* Parry. Coast Ranges north of San Francisco Bay, to the redwood region of Mendocino County.

51. *Ceanothus hirsutus* Nutt. (including *C. oliganthus* Nutt.). Range uncertain; southern Coast Ranges; perhaps southward into Lower California.

52. *Ceanothus incanus* T. and G. Coast Ranges from Humboldt County to the Santa Cruz Mountains, mainly in the redwood region.

53. *Ceanothus integerrimus* H. and A. Deerbrush. Mount Shasta region, south in the Coast Ranges to the Santa Cruz Mountains; lower yellow pine belt of Sierra Nevada; var. *puberulus* (Greene) Abrams, in the mountains of southern California. According to Mrs. Brandegee (10, p. 184), the species ranges southeastward to southern Arizona. An important species in chaparral and as undergrowth in coniferous forest. Deciduous.

54. *Ceanothus megacarpus* Nutt. Near the coast, Santa Ynez to Santa Ana Mountains.

55. *Ceanothus Palmeri* Trelease. Ventura County to the Cuyamaca Mountains and perhaps farther south.

56. *Ceanothus papillosus* T. and G. Of limited range; Santa Cruz Mountains to Santa Lucia Mountains. Grows in the Monterey region with an interesting group of endemics and species of restricted range, including *C. rigidus*, *Arctostaphylos hookeri*, *A. pumila*, and *A. vestita*.

57. *Ceanothus parryi* Trelease. Coast Ranges; Napa and Solano Counties northward to the redwood region of western Mendocino and Humboldt Counties. Deciduous.

58. *Ceanothus parvifolius* (Wats.) Trelease. Central and southern Sierras; conifer-forest chaparral. Deciduous.

59. *Ceanothus pinetorum* Coville (including *C. jepsonii* Greene). Coast Ranges; Lake County to Mount Tamalpais; also in the southern Sierras (Tulare County).

60. *Ceanothus prostratus* Benth. Squaw carpet; mahala mats. North Coast Ranges, Mount Shasta to the San Francisco Bay region; pine belt of the Sierra Nevada. Habit and habitat of *C. diversifolius*, except that toward its southern limit in the Coast Ranges it tends to become erect (var. *divergens* K. Brandegee).

61. *Ceanothus rigidus* Nutt. Limited in range; Marin County to Monterey. (See No. 56.)

62. *Ceanothus sanguineus* Pursh. A northern species reaching the Siskiyou Mountains in northern California; conifer-forest chaparral. Deciduous.

63. *Ceanothus sorediatus* H. and A. Coast Ranges; Napa and Solano Counties to northern Santa Barbara County. Somewhat like *C. cuneatus* in its habits, but preferring more mesophytic situations; coming up thickly like *C. thyrsiflorus* after fire in the redwood forest.

64. *Ceanothus spinosus* Nutt. Coast region of southern California from Santa Barbara County to Orange County. One of the largest members of the genus, sometimes arborescent. Partly evergreen.

65. *Ceanothus thyrsiflorus* Esch. Blue-blossom; California lilac. An abundant species of the redwood region from the northern boundary of the State to the Santa Lucia Mountains; temporary, forming dense thickets after fires.

66. *Ceanothus tomentosus* Parry. Sierras (Amador County) southward to the San Bernardino Mountains and San Diego.

67. *Ceanothus velutinus* Dougl. British Columbia to California; south in the Coast Ranges to Marin County, and in the Sierras to Kern County; eastward to the Rocky Mountains. A very important species of the conifer-forest chaparral, with its companions forming forest undergrowth as well.

68. *Ceanothus verrucosus* Nutt. Vicinity of San Diego, southward into northern Lower California.

CORNACEÆ.

69. *Garrya elliptica* Dougl. Quinine bush. Coast Ranges from Oregon to the Santa Lucia Mountains. Usually present in small number in the climax chaparral; seldom abundant.

70. *Garrya fremontii* Torr. Inner Coast Ranges and Sierra Nevada to San Jacinto Mountains. More closely identified with the conifer forest than with the climax chaparral.

ERICACEÆ.

71. *Comarostaphylis diversifolia* (Parry) Greene. Southern California and northern Lower California. Representative of a genus almost entirely Mexican and Central American.

72. *Xylococcus bicolor* Nutt. Near the coast; San Diego County and northern Lower California. A rather important climax species within its limited range.

73. *Arctostaphylos andersonii* A. Gray. Manzanita.[1] Of local distribution; Oakland Hills and Santa Cruz Mountains.

74. *Arctostaphylos drupacea* (Parry) n. comb. [*A. pringlei* var. *drupacea* Parry: *Uva-ursi drupacea* (Parry) Abrams]. San Bernardino Mountains to northern Lower California. Belongs to the forest region of the higher mountains.

75. *Arctostaphylos glauca* Lindl. From the San Francisco Bay region and Stanislaus County to Mount San Pedro Martir in Lower California. One of the most characteristic and conspicuous members of the climax chaparral of the southern half of the State. Generally scattered among other shrubs, often *Adenostoma*, and standing out conspicuously by reason of its large size, smooth rounded form, and light gray foliage. Probably attains a larger size than any other species of manzanita.

76. *Arctostaphylos hookeri* Don. Near the coast, from San Francisco to San Luis Obispo County; in the Monterey region growing with other species of restricted range. (See No. 56.)

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[1] The name "Manzanita" is applied to all the species indiscriminately; also to the closely related Nos. 71 and 72.

77. *Arctostaphylos manzanita* Parry. Mountains of the northern half of the State, from the region of San Francisco Bay and Stanislaus County into Oregon; almost complementary in range to *A. glauca*, and of equal or greater importance in the climax chaparral.

78. *Arctostaphylos mariposa* Dudley. Sierra foothills and to some extent in the forest region. Of considerable importance where it occurs.

79. *Arctostaphylos montana* Eastwood. Central Coast Ranges, very local; on Mount Tamalpais, where it is apparently confined to the outcrops of serpentine, which are avoided by other species of the genus growing on the mountain.

80. *Arctostaphylos myrtifolia* Parry. Near Ione, Amador County. Known only from the type locality.

81. *Arctostaphylos nevadensis* A. Gray. Upper forest region of the Sierra Nevada; extreme northern California, the mountains of Trinity County, and in the Cascades of Oregon. A very low, spreading shrub, of considerable importance successionally in the high mountain forest regions.

82. *Arctostaphylos nummularia* A. Gray. Outer north Coast Ranges; Santa Cruz Mountains; Mount Tamalpais to Mendocino County. Characteristic of the Mendocino "white plains;" not important in the chaparral.

83. *Arctostaphylos parryana* Lemmon. Southern Sierras and Mount Pinos to the San Bernardino Range.

84. *Arctostaphylos patula* Greene. Cascades of Oregon; eastward to the Blue Mountains (northeastern Oregon) and Utah; south in California to Trinity County in the Coast Ranges, throughout the middle altitudes of the Sierras, extending to Mount San Jacinto. The most important species of the genus in the upper conifer-forest chaparral.

85. *Arctostaphylos pumila* Nutt. Endemic in the Monterey region, growing with other local species already noted (see No. 56). A low, spreading shrub, resembling *A. nevadensis* in habit; an important sand-binder on the dunes of Monterey Bay.

86. *Arctostaphylos pungens* H. B. K. Southern California (San Bernardino and Cuyamaca Mountains) and Lower California to southwestern Colorado, Arizona, and Central Mexico. Conifer-forest chaparral. An important species in the dilute chaparral of the Santa Catalina Mountains in Arizona.

87. *Arctostaphylos stanfordiana* Parry. Of limited range in the inner north Coast Ranges from Mount Diablo to Mendocino County. A rather rare species of the climax chaparral, conspicuous by reason of its yellow-green foliage.

88. *Arctostaphylos tomentosa* (Pursh) Dougl. Southern British Columbia through western Washington and Oregon and the Coast Ranges and Sierras of California to Lower California. Probably the most widely distributed member of the genus except *A. uva-ursi* and possibly *A. pungens*. Extremely variable; several more or less well marked species have been segregated, and the synonymy of the group is confused. An important member of the chaparral, mainly in the climax type; frequently the only manzanita present, and in such cases forming the bulk of the growth of the less xerophytic situations.

89. *Arctostaphylos vestita* Eastwood. Endemic in the Monterey region, growing with other local species already noted (see No. 56).

90. *Arctostaphylos viscida* Parry. East slopes of the inner north Coast Ranges and the Sierra foothills; northward to southern Oregon. An important member of the chaparral of the digger and lower yellow pine zones; forming a very beautiful gray-green cover when in pure growth.

HYDROPHYLLACEÆ.

91. *Eriodictyon californicum* (H. and A.) Torr. Yerba santa. Coast Ranges and lower Sierras. Belongs mainly with the climax chaparral; infrequent, however, in dense brush; characteristic where climax conditions have been disturbed; frequent along roads and trails in the chaparral. Three other species of *Eriodictyon* occasionally occur in the chaparral, but have been excluded from the category of dominants.

THE SECONDARY SPECIES.

In the following paragraphs the normal undergrowth of the broad-sclerophyll forest and the climax chaparral is presented. In addition a list of incidental species might be compiled and extended indefinitely. Some of these are of considerable importance, one group particularly so. This includes species that belong properly to the early stages of primary and secondary successions, remaining as relicts in the climax or subclimax. They have been considered at some length in the section dealing with development.

A complete list of the forest undergrowth is here impracticable, since the flora is so different in various parts of the State. This is especially true in the outer Coast Ranges, where a large element of the herbaceous flora of the redwood forest would have to be included. In the central Coast Ranges, away from redwood dominance, the following shrubs are important as undergrowth:

Holodiscus discolor var. ariæfolius (Wats.) Jepson.
Rubus vitifolius C. and S.
Symphoricarpos racemosus Michx.

In the lowest stratum *Aspidium rigidum* var. *argutum* Eat. and *Micromeria chamissonis* (Benth.) Greene are prominent throughout the year, and species of *Fritillaria, Calochortus, Trillium, Smilacina,* and other spring-flowering genera are conspicuous for a brief time. A complete list from a single typical locality is given on page 38.

The herbaceous vegetation of the normal undisturbed chaparral is exceedingly scanty, both in number of species and of individuals. Further, few of the species that do occur can be considered as peculiar to the chaparral. All of them could without serious inaccuracy be consigned to the category of incidentals. However, a few have been selected which seem to be more characteristic of the chaparral than of any other community. All of these are perennials. Naturally they are more abundant in the less xerophytic situations. This list is fairly complete only for the localities with which I am most familiar. Doubtless other species would be added with more extended observation. Several have the peculiar habit described under *Zygadenus fremontii.*

List III.—Herbaceous Species of the Chaparral.

92. *Gymnogramme triangularis* Kaulf. Gold-back fern. Rather frequent in the more mesophytic situations.

93. *Pellaea mucronata* (Eaton) Maxon [*P. ornithopus* Hook.]. Bird-foot fern. Characteristic of especially dry situations, often where the chaparral is thin.

94. *Zygadenus fremontii* Torr. Frequent under the chaparral bushes in suppressed condition, not flowering in such state; conspicuous after fire or clearing, flowering freely and seemingly suddenly increasing in abundance.

95. *Xerophyllum tenax* Nutt. Turkey-beard. Decidedly infrequent, but very conspicuous after fires.

96. *Chlorogalum pomeridianum* (Ker.) Smith. Soapweed. Similar in habits to the last.

97. *Brodiæa californica* Jepson. Twining brodiæa. An anomalous member of the genus in its climbing habit; straggling and weakly twining upon chaparral bushes; lower altitudes of the Sierra Nevada.

98. *Lilium washingtonianum* Kellogg. Washington lily; chaparral lily. In the chaparral of the Sierras and in the mountains of northern California, and northward to the Columbia River.

99. *Aster radulinus* A. Gray. Growing in suppressed condition; flowers after clearing.

BIBLIOGRAPHY.

(1) Abrams, L. R. 1910. A phytogeographic and taxonomic study of the southern California trees and shrubs. Bull. N. Y. Bot. Gard. 6; No. 21: 300–485.

(2) ——— 1914. Uva-ursi. In North American Flora, vol. 29, pt. 1: 92–101. New York Botanical Garden.

(3) ——— and F. J. Smiley. 1915. Taxonomy and distribution of *Eriodictyon*. Bot. Gaz. 60: 115–133.

(4) Adamovic, Lujo. 1909. Die Vegetations-verhältnisse der Balkanländer. Engler und Drude: Die Vegetation der Erde, XI.

(5) Adams, C. C. 1902. Southeastern United States as a center of geographical distribution of flora and fauna. Biol. Bull. 3, No. 3.

(6) Barber, J. H. 1898. A glimpse of the San Gabriel forest reservation. The Forester, 4: 240–242.

(7) Beck von Mannagetta, G. R. 1901. Die Vegetations-verhältnisse der illyrischen Länder. Engler und Drude: Die Vegetation der Erde, IV.

(8) Bergen, J. Y. 1903. The macchie of the Neapolitan coast region. Bot. Gaz. 35: 350–362; 416–426.

(9) Boerker, R. H. 1915. The reforestation of brush fields in northern California. Proc. Soc. Amer. Foresters 10: 284–293; also For. Quart. 13: 15–24.

(10) Brandegee, K. 1894. Studies in *Ceanothus*. Proc. Calif. Acad. Sci., ser. 2, vol. 4: 173–222.

(11) Brandegee, T. S. 1889. Plants from Baja California. Proc. Calif. Acad. Sci., ser. 2, vol. 2: 117–216.

(12) ——— 1891-92. The vegetation of "burns." Zoe 2: 118–122.

(13) ——— 1893–94. The southern extension of the Californian flora. Zoe 4: 199–210.

(14) Branner, J. C. 1909. Santa Cruz folio. U. S. Geol. Sur., Geol. Folio No. 163.

(15) Briggs, L. J., and H. L. Shantz. 1911. A wax seal method for determining the lower limit of available soil moisture. Bot. Gaz. 51: 210–219.

(16) Cannon, W. A. 1911. The root habits of desert plants. Carnegie Inst. Wash. Pub. No. 131.

(17) ——— 1913. A note on a chaparral-forest relation at Carmel, California. Plant World 16: 36–38.

(18) ——— 1914. Specialization in vegetation and in environment in California. Plant World 17: 223–237.

(19) ——— 1914. Tree distribution in central California. Pop. Sci. Mo. 85: 417–424.

(20) ——— 1918. The evaluation of the soil-temperature factor in root growth. Plant World 21: 64-67.

(21) Clements, F. E. 1916. Plant succession. Carnegie Inst. Wash. Pub. No. 242.

(22) ——— 1920. Plant Indicators: The relation of plant communities to process and practice. Carnegie Inst. Wash. Pub. No. 290.

(23) Cooper, W. S. 1917. Redwoods, rainfall, and fog. Plant World 20: 179–189.

(24) Davy, J. B. 1902. Stock ranges of northwestern California. U. S. Dept. Agr., Bur. Plant Ind. Bull. 12.

(25) Diels, L. 1906. Die Pflanzenwelt von west-Australien südlich des Wendekreises. Engler und Drude: Die Vegetation der Erde, VII.

(26) Drude, O. 1890. Handbuch der Pflanzengeographie.

(27) Dudley, W. R. 1901. Zonal distribution of trees and shrubs in the southern Sierra. Sierra Club Bull. 3, No. 24: 298–312.

(28) Eastwood, Alice. 1903. Notes on *Garrya*, with descriptions of new species and key. Bot. Gaz. 36: 456–463.

(29) Engler, A. 1902. Die pflanzengeographische Gliederung Nordamerikas. Abdruck, aus dem Notizblatt des königl. bot. Gart. Appendix IX.

(30) Foster, H. D. 1912. Interrelation between brush and tree growth on the Crater National Forest, Oregon. Proc. Soc. Amer. Foresters, vol. 7, No. 2: 212–225.

(31) Fuller, G. D., and A. L. Bakke. 1918. Raunkiaer's "life forms," "leaf-size classes," and statistical methods. Plant World 21: 25–37.
(32) Gemoll, Kurt. 1902. Anatomisch-systematische Untersuchung des Blattes aus den Triben: Rhamneen, Colletieen und Gouanieen. Beih. zu Bot. Cent. 12: 351–424.
(33) Greene. E. L. 1893. Vegetation of the summit of Mount Hamilton. Erythea 1: 77–97.
(34) ——— 1893. Vegetation of Mount Diablo. Erythea 1: 166–179.
(35) Grinnell, Joseph. 1908. The biota of the San Bernardino Mountains. Univ. Calif. Pub. in Zool. 5: 1–170.
(36) Guttenberg, Hermann Ritter von. 1907. Anatomisch-physiologische Untersuchungen über das immergrüne Laubblatt der Mediterranflora. Eng. Bot. Jahrb. 38: 383–444.
(37) Haefner, H. E. 1912. Chaparral areas on the Siskiyou National Forest. Proc. Soc. Amer. Foresters 7: 82–95.
(38) Hall, H. M. 1902. A botanical survey of San Jacinto Mountain. Univ. Calif. Pub. in Bot. 1: 1–144.
(39) ——— 1912. A Yosemite flora.
(40) Hansen, George. 1897. *Ceanothus* in landscape of the Sierra Nevada. Garden and Forest 10: 102–103.
(41) Harshberger, J. W. 1911. Phytogeographic survey of North America. Engler und Drude; Die Vegetation der Erde, XIII.
(42) Herzog, Theodor. 1903. Anatomisch-systematische Untersuchung des Blattes der Rhamneen aus den Triben: Ventilagineen, Zizypheen und Rhamneen. Beih. zu Bot. Cent. 15: 95–207.
(43) Howell, Thomas. 1903. Flora of Northwest America.
(44) Jepson, W. L. 1891. Botany of the Marysville Buttes, Sacramento Valley. Bull. Torr. Bot. Club 18: 317–327.
(45) ——— 1893. The mountain region of Clear Lake. Erythea 1: 10–16.
(46) ——— 1899. Vegetation of the summit of Mount St. Helena. Erythea 7: 105–113.
(47) ——— 1910. The silva of California. University Press, Berkeley.
(48) ——— 1911. Flora of western middle California. 2d edition.
(49) ——— (Date?) Regeneration in manzanita. Madroño 1: 3–11.
(50) Leiberg, J. B. 1899. San Bernardino Forest Reserve. U. S. Geol. Sur., 19th Ann. Rep., pt. 5: 359–365.
(51) ——— 1899. San Gabriel Forest Reserve. U. S. Geol. Sur., 19th Ann. Rep., pt. 5: 367–371.
(52) ——— 1899. San Jacinto Forest Reserve. U. S. Geol. Sur., 19th Ann. Rep., pt. 5: 351–357.
(53) ——— 1900. San Bernardino Forest Reserve. U. S. Geol. Sur., 20th Ann. Rep., pt. 5: 429–454.
(54) ——— 1900. San Jacinto Forest Reserve. U. S. Geol. Sur., 20th Ann. Rep., pt. 5: 455–478.
(55) ——— 1900. San Gabriel Forest Reserve. U. S. Geol. Sur., 20th Ann. Rep., pt. 5: 409–428.
(56) ——— 1902. Forest conditions in the northern Sierra Nevada, California. U. S. Geol. Sur., Prof. Paper 8.
(57) Livingston, B. E. 1910. Relation of soil moisture to desert vegetation. Bot. Gaz. 50: 241–256.
(58) McAdie, A. G. 1902. Wet and dry seasons in California. U. S. Dept. Agr. Year Book, 1902: 187–204.
(59) ——— 1903. Climatology of California. U. S. Weather Bur. Bull. L.
(60) McKenney, R. E. B. 1901. Notes on plant distribution in southern California. Beih. zu Bot. Cent. 10: 166–178.
(61) Merriam, C. Hart. 1893. Notes on the distribution of trees and shrubs in the deserts and desert ranges of southern California, southern Nevada, northwestern Arizona, and southwestern Utah. U. S. Dept. Agr., Div. Biol. Surv., N. A. Fauna No. 7: 285–343.
(62) ——— 1899. Results of a biological survey of Mount Shasta, California. U. S. Dept. Agr., Div. Biol. Surv., N. A. Fauna No. 16.

(63) Merriam, C. Hart. 1905. The Indian population of California. Amer. Anthrop., n. s., 7: 596–606.
(64) Miller, L. C. 1906. Chaparral as a watershed cover in southern California. Proc. Soc. Amer. Foresters 1: 147–157.
(65) Moore, Barrington. 1917. The moisture withholding power of soils. Jour. For. 15: 110–117.
(66) Munns, E. N. 1916. Results of the effect of chaparral and forest cover on meteorological conditions. Sci. 44: 759–760.
(67) ——— 1919. Some biological and economic aspects of chaparral. Jour. of Forestry 17: 9–14.
(68) ——— 1920. Chaparral cover, run-off, and erosion. Jour. of Forestry 18: 806–814.
(69) Nichols, G. E. A working basis for the ecological classification of plant communities. Ecology: in press.
(70) Niedenzu, Franz. 1890. Über der anatomischen Bau der Laubblätter der Arbutoideæ und Vaccinioideæ in Beziehung zu ihrer systematischen Gruppierung und geographischen Verbreitung. Eng. Bot. Jahrb. 11: 134–263.
(71) Parish, S. B. 1903. A sketch of the flora of southern California. Bot. Gaz. 36 203–222; 259–279.
(72) ——— 1917. An enumeration of the pteridophytes and spermatophytes of the San Bernardino Mountains, California. Plant World 20: 163–178; 208–223; 245–259.
(73) Piper, C. V., and R. K. Beattie. 1915. Flora of the Northwest Coast. State College, Pullman, Wash.
(74) Plummer, F. G. 1911. Chaparral. U. S. Dept. Agr., For. Serv. Bull. 85.
(75) Purdy, Carl. 1897. The chemise world. Garden and Forest 10: 72; 83.
(76) Purpus, C. A. T. 1897. Die Chaparral-region der südwestlichen Sierra Nevada von Californien. Mitt. d. deutsche dendrol. Ges. No. 6.
(77) Reed, W. G., and J. B. Kincer. 1917. Average annual precipitation map of the United States. Mo. Wea. Rev. 45, No. 7.
(78) Reiche, K. 1907. Grundzüge der Pflanzenverbreitung in Chile. Engler und Drude: Die Vegetation der Erde, VIII.
(79) Sargent, C. S. 1905. Manual of the trees of North America.
(80) Schimper, A. F. W. 1903. Plant geography upon a physiological basis. Transl. by Groom and Balfour.
(81) Shreve, Forrest. 1915. The vegetation of a desert mountain range as conditioned by climatic factors. Carnegie Inst. Wash. Pub. No. 217.
(82) Shull, C. A. 1916. Measurement of the surface forces in soils. Bot. Gaz. 62: 1–31.
(83) Smith, W. G. 1913. Raunkiaer's "life-forms" and statistical methods. Jour. Ecol. 1: 16–26.
(84) Solereder, Hans. 1908. Systematic anatomy of the dicotyledons. Transl. by Boodle and Frisch.
(85) Sterling, E. A. 1904. Chaparral in northern California. For. Quart. 2: 209–214.
(86) Sudworth, G. B. 1900. Stanislaus and Lake Tahoe Forest Reserves and adjacent territory. U. S. Geol. Sur., 21st Ann. Rep., pt. 5: 499–561.
(87) ——— 1908. Forest trees of the Pacific Slope. U. S. For. Serv.
(88) Transeau, E. N. 1905. Forest centers of eastern America. Amer. Nat. 39: 875–889.
(89) Trelease, W. 1895–97. Rhamnaceæ. In Asa Gray; Synoptical flora of North America: 401–419.
(90) Warming, E. 1909. Œcology of Plants. Trans. by Groom and Balfour.
(91) Wilkomm, M. 1896. Grundzüge der Pflanzenverbreitung auf der iberischen Halbinsel. Engler und Drude: Die Vegetation der Erde I.

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